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University — Université

University of Alberta

Degree for which thesis was presented — Grade pour lequel cette thèse fut présentée

M.Sc.

Year this degree conferred — Année d'obtention de ce grade

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LIFE HISTORY AND ECOLOGY OF AQUATIC INSECTS ASSOCIATED WITH SHIFTING SAND AREAS, WITH SPECIAL REFERENCE TO THEIR CONTRIBUTION TO MACROINVERTEBRATE BIOMASS AND PRODUCTION IN RIVERS.

by

Daniel Anton Soluk

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

Department of Zoology

EDMONTON, ALBERTA

Fall, 1983

THE UNIVERSITY OF ALBERTA

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ABSTRACT

Benthic macroinvertebrates associated with areas of shifting sand in a river in central Alberta, Canada, were studied over two years. The life history and ecology of the three dominant species (*Robackia demeijerei*, *Rheosmittia sp.*, and *Pseudiron centralis*) were intensively studied.

Larvae of the chironomids *R. demeijerei* and *Rheosmittia* were associated with interstitial environments in shifting sand, where they often attained densities greater than 50,000 larvae/m^2. *Robackia demeijerei* was univoltine with an extended emergence pattern; *Rheosmittia sp.* was bivoltine. Laboratory experiments indicated that larvae of both species actively selected for coarse sand (0.50 to 2.00 mm). *Rheosmittia sp.* larvae appeared to feed primarily on diatoms, while *R. demeijerei* larvae exhibited uncertain dietary preferences.

Larvae of the predaceous heptageniid mayfly *Pseudiron centralis* were associated with shifting sand areas only in the later developmental stages, early stage larvae were associated with marginal areas. *P. centralis* larvae foraged across the surface of the sediments, feeding primarily on larvae of two chironmid species. *Pseudiron centralis* larvae occurred in low densities (<4 larvae/m^2) and the population exhibited a random dispersion pattern on shifting sands. The movement of larvae from marginal areas to shifting sand areas during development was hypothesized as a mechanism which allowed either an escape from potential predators or

the exploitation of the abundant and accessible chironomid fauna of shifting sand.

Overall, macroinvertebrate numbers were high on shifting sand, although both biomass and production were relatively low on a unit area basis. Shifting sand areas occupy a large proportion of the bed in larger rivers, and it is suggested that these areas make significant contributions to functional processes in river ecosystems.

ACKNOWLEDGEMENTS

I thank Dr. Hugh F. Clifford for his support and for valuable suggestions made during the course of this study. I extend special thanks to Drs. Jan J.H. Ciborowski, Paul A. Murtaugh and Mr. Richard J. Casey, for critically reviewing parts of this study. Thanks to my fellow graduate students in aquatic ecology Dr. Robert Baker, Jay Babin, Vytenis Gotceitas, John Richardson, and Edward Riley; all of which contributed in frank interchanges of ideas.

Thanks to my brother Richard A. Soluk for able and untiring assistance in the field; also to Teresa Lovell, Roberta Miller and Elizabeth Thompson for assistance in both the laboratory and field. Special thanks to Mrs. Gertrude Hutchinson, both for her patience and technical assistance. I also acknowledge the use of computing terminals provided by Drs. F.S. Chia and E.E. Prepas.

Thanks to Dr. John F. Addicott for his valuable insights in both scientific and personal matters. Thanks also to Dr. Douglas A. Craig for his interest in the morphology of these psammophilous invertebrates.

Most especially I would thank my wife Laureen J. Soluk not only for her untiring technical assistance, but also for her love and support, without which this study would not have been possible.

Financial assistance was provided by a NSERC operating grant to Dr. H.F. Clifford and a Boreal Institute For Northern Studies grant to the Author.

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THESIS INTRODUCTION

Rivers have been important to the development and maintenance of both modern and past civilizations. Examination of a map of the world quickly confirms that most of the major cities are located in close proximity to large navigable rivers. Despite the importance of these rivers in transportation, waste disposal, electrical generation, fisheries, and as sources of freshwater for both human and agricultural consumption, the biota of these systems has seldom been studied.

Large lowland rivers exhibit widely fluctuating discharge, high mean current velocities, and are relatively deep. These characteristics make studies of the biota of these rivers both difficult and expensive, and thus most stream ecologists have focused their research on smaller headwater streams. There are few quantitative studies of the lower reaches of river systems, and generalizations about river ecosystems have often stressed processes that are important primarily in headwater areas.

Most studies carried out in lowland rivers are conducted by or for government agencies, usually with the intent of assessing the impact of some human activity on the biota of a particular river. Thus, most studies of rivers usually have relatively narrow objectives and often only examine organisms that are associated with artificial substrates or one type of habitat in the river bed. The use of artificial substrates has often been criticized, because

the relationship between the communities inhabiting these substrates and those inhabiting natural substrates in the river bed is only poorly understood (Rosenburg and Resh, 1982). When benthic macroinvertebrate communities are examined, usually only those found in riffle or silty backwater areas are considered (Barton, 1980). Although these areas are certainly prominent habitat types, they usually occupy only a small proportion of the mainstream channel of most rivers.

Sand is the dominant substrate material in the bed of most larger lowland rivers (Leopold *et al.*, 1964). A variety of physical and chemical factors, such as the friability of large stones and the crystal structure of silicates, contribute to the dominance of sand-sized material (Leopold *et al.*, 1964).

Hynes (1970) distinguishes between two types of sandy habitats: mixtures of sand and silt, which form a firm substrate, and shifting sands, which form a loosely consolidated soft substrate. Sand and silt areas usually occur marginally as a narrow band roughly paralleling the river banks, and shifting sand areas usually dominate the central channel.

Shifting sand areas have generally been considered hostile environments for benthic macroinvertebrates, and have been indicated as supporting only a few species and individuals (Hynes, 1970). This view has generally been confirmed by most studies that have examined shifting sand

areas in rivers (Berner, 1951; Monakov, 1968; Northcote *et al.*, 1976; Seagle *et al.*, 1976). However, studies of the fauna of some large rivers in the U.S.S.R. (Zhadin and Gerd, 1961), and intensive studies carried out on the Athabasca River (Barton and Lock, 1979; Barton, 1980) have indicated that large numbers of organisms could be found in shifting sand areas.

My study was undertaken to examine the potential contribution of shifting sand areas to both macroinvertebrate biomass and production in river systems. It was reasoned that if the small macroinvertebrates associated with shifting sand areas occurred in high densities and exhibited high generation turnover rates then these areas could be potential sources of a significant proportion of the total secondary production in river systems.

The Sand River in east-central Alberta was used as a representative river since its moderate size allowed a relatively intensive quantitative study to be conducted with a reasonable degree of continuity and effort. Although it is not a large river, it possesses the macroinvertebrate fauna typical of large rivers in North America, including many species considered to be quite rare.

Since little is known of the biology of psammophilous invertebrates in rivers, the first two chapters of this work describe various aspects of the life history and ecology of the three dominant species of macroinvertebrate found in

shifting sand habitats in the Sand River. In the third chapter, using data on the life history and patterns of abundance reported in the first two chapters, I estimate the potential macroinvertebrate production from shifting sand areas and attempt to evaluate the contribution and role of these areas in river ecosystems.

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I. THE LIFE HISTORY AND ECOLOGY OF *Pseudiron centralis* McDunnough (EPHEMEROPTERA: HEPTAGENIIDAE), A PREDACEOUS MAYFLY ASSOCIATED WITH SANDY SUBSTRATES IN RIVERS.

ABSTRACT

This study examines aspects of the life history, distribution, abundance, and behavior of *Pseudiron centralis* McDunnough in a river in central Alberta. The population studied exhibited a univoltine summer life cycle: larvae hatched in late April, developed rapidly, emerged as adults in late June and throughout July, and spent the remainder of the year in the egg stage. *Pseudiron centralis* larvae were found in association with three types of substrate in the river bed: shifting sand, marginal sand, and gravelly sand. The substrate associations of larvae changed over the course of development; stage I larvae were associated with marginal sand areas, and stage III and IV larvae were associated with shifting sand areas. Larval density was found to be relatively low (<4 larvae/m^2), however, larval mortality also appeared to be low. Stage III & IV larvae exhibited a random dispersion pattern on shifting sand substrates. Secondary production of *P. centralis* larvae was estimated to be 18.4 and 5.67 mg/m^2/yr in 1980 and 1981 respectively. *Pseudiron centralis* larvae were active epibenthic predators, appearing to feed primarily on psammophilous chironomid larvae. An experiment examining spacing behavior in *P. centralis* larvae suggested that interactions between individuals were probably not important determinants of larval density or distribution. Substrate selection experiments indicated that stage III *P. centralis* larvae avoided gravel, but did not indicate discrimination against

fine sand or silt. Stage I larvae are probably restricted to marginal sand areas because they cannot cope with the physical stresses in shifting sand areas. The shift in association to shifting sand areas is hypothesized to be a mechanism that allows the animal to exploit either the greater prey availability or the lower numbers of potential predators and competitors in these areas.

INTRODUCTION

Sand is a dominant component in the bed of most large rivers. However, very little is known of the ecology of organisms and the nature of communities found in sandy habitats in large rivers.

Several species of Ephemeroptera are associated with the sandy substrates of large rivers. These species have been of interest to systematists because many exhibit aberrant morphologies that make their phylogenetic placement difficult. Behaviorally, the larvae of many of these species are distinct from the majority of Ephemeroptera in being predaceous. One species (*Dolania americana* Edmunds and Traver) has been studied in detail (Tsui and Hubbard, 1979; Harvey *et al.*, 1980; Sweeney and Vannote, 1982), but knowledge of most sand-dwelling mayflies is restricted to anecdotal comments by collectors. Knowledge of the ecology of these species could contribute greatly toward an increased understanding of important ecological processes in one of the dominant habitat types in the lower reaches of most river systems.

Pseudiron larvae are associated with sandy river beds in medium to large rivers over much of North America (Edmunds *et al.*, 1976). The carnivorous behavior of larval *Pseudiron* and some aspects of their foraging behavior were discussed by Edmunds *et al.* (1976). Tsui and Hubbard (1979) speculated on the nature of habitat partitioning between *Pseudiron meridionalis* Traver and another predaceous mayfly,

Dolania americana (*P. meridionalis* occupies the surface of the sand while *D. americana* burrows beneath it).

There are two described species of *Pseudiron*: *P. meridionalis* Traver occurs in the southeastern United States, and *P. centralis* McDunnough is found in western and central North America (Edmunds *et al.*, 1976). *Pseudiron centralis* is found in all major drainage systems in Alberta.

This study examines aspects of the life history and ecology of *P. centralis* in a medium-sized river in central Alberta, Canada. Two approaches were used: (1) a field-correlative approach was utilized to assess the life history and to elucidate patterns of distribution and abundance of this species; and (2) a laboratory-experimental approach was used to assess some of the proximal determinants of the observed patterns.

STUDY SITE

The Sand River is located on the southern edge of the mixed boreal forest of Alberta (Plate I.1). It drains approximately 5000 km² of largely forested land and has its headwaters in the Department of National Defense Primrose Lake Air Weapons Range. The Sand River is the major tributary of the the Beaver River System in Alberta and supplies approximately 75% of the total discharge. The Beaver River is a tributary of the Churchill River which drains into Hudson Bay.

Plate I.1 Aerial view of the mouth of the Sand River (A= Sand River; B= Beaver River). Study area is indicated by the two arrows. Insert indicates location in Alberta.

During the study period the mean discharge of the Sand River was approximately 12 m^3/s with a range from 1.5 to 42.9 m^3/s (Environment Canada, 1981; and unpublished data courtesy of Environment Canada, Water Survey of Canada).

The bed of the Sand River is composed primarily of sand derived from the extensive deposits of this material found in Northeastern Alberta. In the mainstream channel, sand forms moving dunes 6 to 15 cm in height, which may be riding on larger dunes with very long wavelengths and heights of over 50 cm. Occasional gravel bars occur in the bed and there is a narrow marginal band of silty deposits.

The study area (54° 23'N; 111°02'W) was at the mouth of the Sand River (Plate I.1). Thalweg current velocities ranged from 40 to 150 cm/s at the study site, but were usually about 60 cm/s. Immediately upstream of its mouth, the Sand River is 30 to 50 m in width with a maximum depth of 1.5 to 2 m; below its mouth the width of the flow widens and the mean depth decreases to between 1 and 1.5m.

At the study site the Sand River is quite warm with an average summer temperature of approximately 20°C; the maximumum temperature recorded was 27°C.

MATERIALS AND METHODS

Field Studies

Four major substrate types were recognized: "shifting sands" (SS), "marginal sands" (MS), "gravelly sands" (GS),

and "silt" (SI). These substrate types were defined using the visual and tactile criteria presented in Table I.1.

Data on the distribution and abundance of *P. centralis* larvae were obtained from samples taken along ten transects established at 5 m intervals along a 50 m reach at the mouth of the Sand River. Samples were taken at intervals determined by the availability of the different substrate types along each of these transects. Samples were obtained from the middle area of those substrates that occurred in narrow bands parallel to the banks and at intervals of approximately 5, 10, 20, and 30 m from the bank wherever possible in SS areas.

Sampling was primarily bi-weekly throughout the open water season (April to November) in 1980, from April to the end of July in 1981, and on one date in June 1982.

A Surber sampler (mesh 0.243 mm) modified with a handle and a extra long net bag was the chief sampling device used throughout the study. The depth and velocities encountered precluded the use of closed cylinder type samplers. Samples were collected by disturbing the substrate, within a 930 cm^2 area defined by the sampler, with the foot for 30 seconds. Samples were placed in jars and preserved with 95% ethanol.

In the laboratory, organic material was separated from inorganic material by elutriation, examined under a dissecting microscope at 12X magnification, and the *P. centralis* larvae removed. A standard "D" frame dipnet (mesh size 0.5 mm) was used to collect additional larvae for

Table I.1 Criteria for identifying the prominent substrate types in the Sand River.

Substrate Category	Visual and Tactile Criteria
Silt (SI)	soft sticky texture, abundant visible silt, dark grey or black color
Marginal Sand (MS)	firm fine-grained texture, some visible silt, few sand particles in active motion
Gravelly Sand (GS)	firm coarse texture, abundant gravel apparent, few sand particles in active motion
Shifting Sand (SS)	soft loose texture, no apparent silt, actively moving sand dunes

life history analysis, dry weight determinations, and experimental analysis.

Larval stages were designated using the criteria of Clifford (1970): stage I larvae lack wing pads, stage II larvae possess wing pads whose length is less than the distance between them, stage III larvae have wing pads longer than the distance between them, and stage IV larvae have the darkened wing pads characteristic of the last larval instar. Head capsule widths were measured at the widest point (just posterior to the eyes). All measurements were made at 25X or 50X magnification using a eyepiece micrometer on a dissecting microscope.

The mean dry weight of larvae was determined from frozen specimens, which were thawed and dried at 60°C for 24 hrs. Weights were measured on a microbalance to the nearest 0.002 mg.

The food habits of *P. centralis* larvae were determined by examination of the foregut of 20 individuals belonging to stage II, III or IV. The contents were quantified by direct counts of the type and number of organisms in the foregut.

To determine fecundity, female subimagoes (reared from larvae kept for a short period in the laboratory) were dissected, and all eggs removed and counted. The eggs of these females were then placed in dechlorinated water and the dimensions measured at irregular intervals over a 24 hour period to determine egg size.

Observations of the behavior of *P. centralis* larvae were carried out in various types of artificial streams.

Experimental Studies

Substrate selection by *P. centralis* larvae was investigated using three different experimental designs, described in the results section. The spacing behavior of these larvae was examined in one experiment. All substrates used in these experiments were natural mineral substrates removed from the bed of the Sand River. Before being used, these substrates were heated to 600°C for 48 hours, dry sieved into the appropriate size class, and washed with distilled water.

RESULTS

Life History

Pseudiron centralis was univoltine in the Sand River (Figs. I.1 and I.2), apparently overwintering in the egg stage. The relatively large first instar larvae of this species (headwidth approximately 0.24 mm, bodylength approximately 0.90 mm) first appeared in late April and were easy to distinguish because compound eyes, ocelli, and gills were not apparent. Neither quantitative nor intense qualitative collecting yielded *P. centralis* larvae in late autumn before the formation of ice.

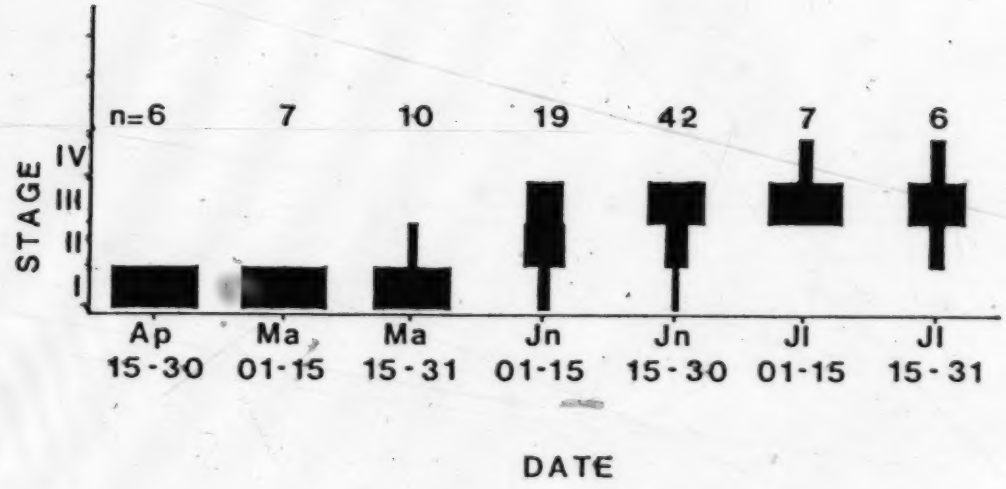

Figure I.1 Larval development of *P. centralis* based on larval stage (see text). Horizontal width of bars represents proportion of larvae in each particular stage.

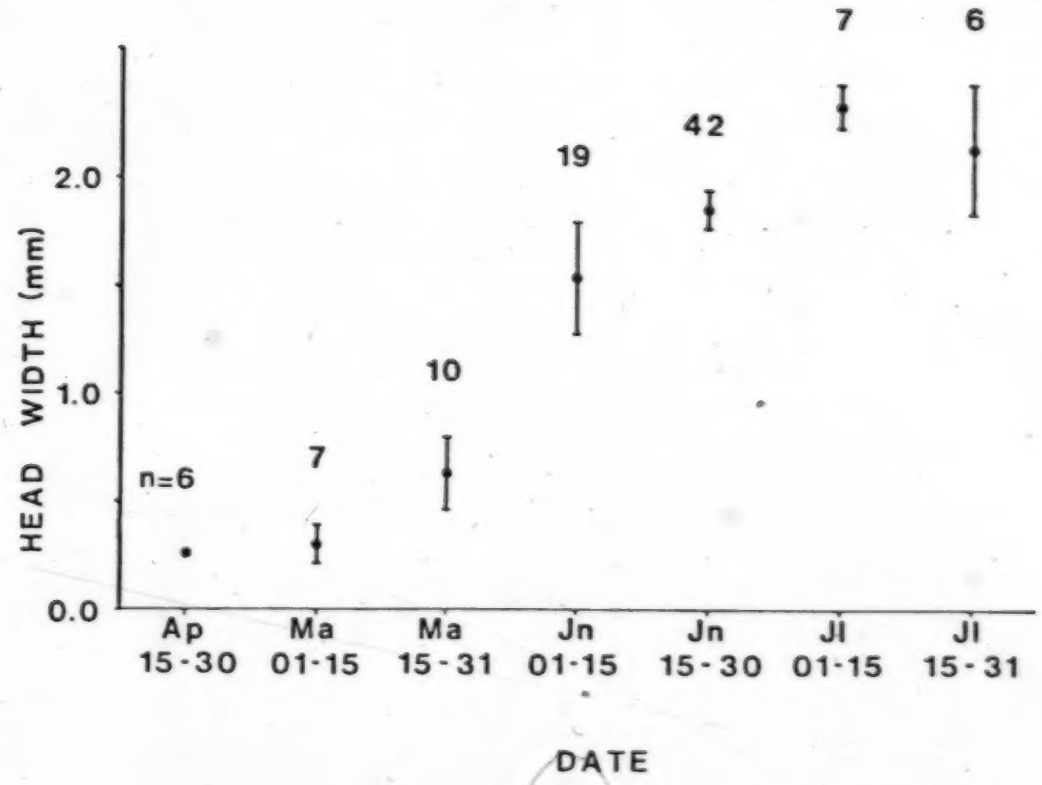

Figure I.2 Larval development of *P. centralis* based on mean larval headwidth. Vertical bars represent one standard error of the mean.

After the larvae hatched, subsequent development was rapid with mature larvae appearing in the population in less than 8 weeks. The low number of stage IV larvae collected is likely an artifact due to the relatively short duration (2 to 3 days under laboratory conditions) of this stage. Adult emergence was not observed at the study site, but the presence of stage IV nymphs indicated emergence from late June to the end of July. This pattern is probably similar over the entire range of this species; all reported adult records of *P. centralis* are from June and July (McDunnough, 1931; Burks, 1953). Thus it appears that *P. centralis* spends most of the year in the egg stage, its life cycle being best described, in the terminology of Clifford (1982), as a univoltine summer cycle

The swarming behavior of adult *Pseudiron* spp. has never been reported, and I was unable to find swarming adults. However, emerging subimagoes and spent imagoes were collected from the water's surface at one locality during mid to late morning.

The fecundity of females appears to be relatively low compared to those recorded for other large mayflies (Brittain, 1982), with 624 and 467 being the total number of eggs encountered in the two females examined. The mean dry weight of eggs was 0.005 mg (S.D.=0.001) based on the weights of five groups of ten eggs.

Needham *et al.* (1935) figure the egg of *Pseudiron sp.* removed from a preserved specimen of an unspecified stage

(presumably subimago or imago). The egg was ellipsoid in shape with dimensions of approximately 0.190 x 0.310 mm. The size and shape of this egg was similar to that of the compressed eggs found within the bodies of female subimagoes of *P. centralis* from the Sand River. However, when I exposed these eggs to water, they rapidly became more rotund, attaining dimensions of approximately 0.33 x 0.41 mm.

One egg was collected from the shifting sand area of the Sand River on Oct. 17, 1981. This egg had approximate dimensions of 0.35 x 0.41 mm, and a number of sand grains were firmly adhering to it. Positive identification of the egg as that of *P. centralis* was possible because the egg enclosed an almost fully developed first instar larvae.

Larval Distribution and Abundance

Pseudiron centralis larvae were restricted to the three types of sandy substrates described in Table I.1; no larvae were collected from silt areas. Larval associations with the sandy substrate types appeared to change during larval development (Fig. I.3).

Contingency table analysis (Zar, 1974) was used to determine whether particular larval stages exhibited associations with particular substrate types (Table I.2). Where significant ($p<0.05$) associations were indicated, subdivision of the contingency table (Zar, 1974) was used to assign particular associations. Data for each stage were assembled only from dates where the stage in question was

Table I.2 Number of samples obtained from the three categories of sandy substrate (SS= shifting sand; MS= marginal sand; and GS= gravelly sand) in which *P. centralis* larvae of particular stages were present or absent.

Stage I Larvae

Samples with larvae:	Substrate Category SS	MS	GS	Total
Absent	71	34	31	136
Present	4	11	6	21
Total	75	45	37	157

Stage II Larvae

Absent	66	33	27	126
Present	10	3	1	14
Total	76	36	28	140

Stage III & IV Larvae

Absent	48	26	24	98
Present	24	2	1	27
Total	72	28	25	125

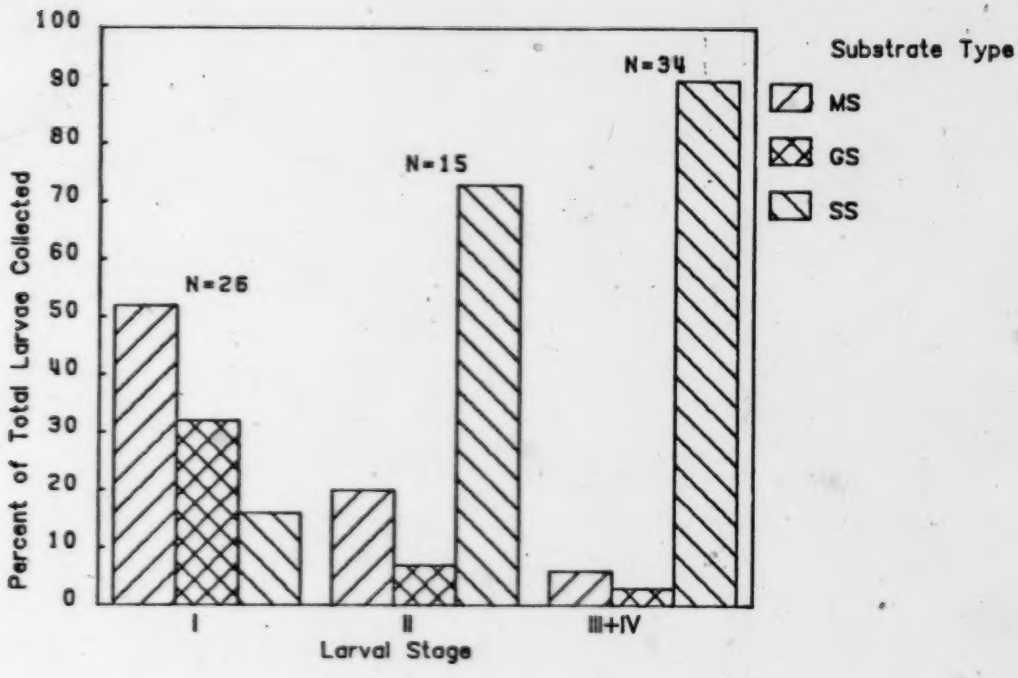

Figure I.3 Number of *P. centralis* larvae obtained from the three categories of sandy substrate: shifting sand (SS), marginal sand (MS), and gravelly sand (GS).

likely to be present (Fig. I.1); stages III and IV were considered together. The analysis indicated that stage I larvae were significantly ($p<0.05$) associated with MS areas and stage III and IV larvae were significantly ($p<0.001$) associated with SS areas. The low number of stage II larvae necessitated a pooling of the MS and GS categories; these larvae exhibited no statistically significant differentiation between this pooled category and SS.

There did not appear to be substantial changes in substrate availability during the larval period in either year of this study; hence, it seems unlikely that the shift in substrate association can be attributed to changes in substrate availability.

Pseudiron centralis larvae occurred at low densities and much effort was required to collect them. Figure I.4 illustrates the mean larval densities in the Sand River in 1980 and 1981. These densities were obtained by summing the density estimates of *P. centralis* on GS, MS, and SS areas weighted with respect to the proportion of river bed that they represent. At the study site the proportions were estimated to be approximately 70% for SS, and 15% each for both MS and GS areas, based on the occurrence of these substrates along the transects. The study site was generally representative of the bed of the Sand River, except that the GS area was somewhat over-represented.

Densities of *P. centralis* larvae remained relatively constant throughout the period of larval development,

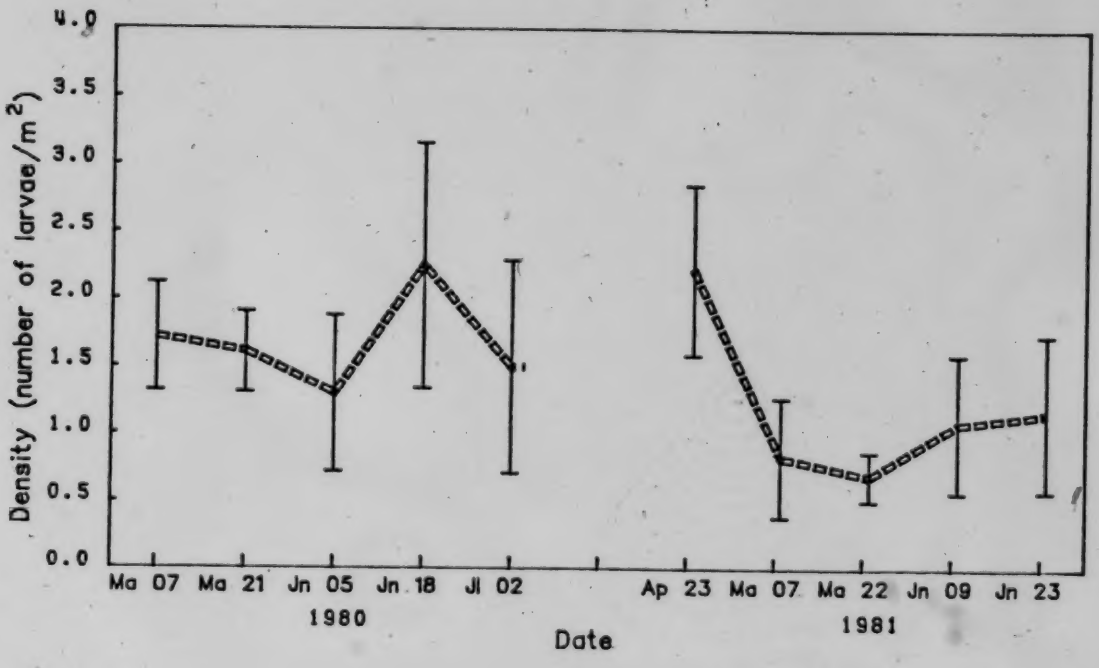

Figure I.4 Mean larval density (±S.E.) of *P. centralis* in the Sand River based on weighted estimates from the three types of sandy substrate.

suggesting relatively low rates of larval mortality. Despite the low density of *P. centralis* larvae, individuals were collected with a high degree of regularity on a per sample or per unit effort basis. A series of 24 samples were collected on June 15, 1982 from SS areas to determine the nature of the dispersion pattern of *P. centralis* larvae on this substrate. Numbers of larvae in each sample (Table I.3) were compared with values that would be expected from a Poisson distribution utilizing the index of dispersion (Southwood, 1978). The analysis indicated that *P. centralis* larvae were randomly distributed (χ^2=28.70, $p>0.10$) over shifting sand areas.

The larval density in 1982 was higher (10.16 larvae/m^2 for all sandy substrates) than during the previous two years (Fig. I.4), but this change was not considered large enough to affect the dispersion pattern of larvae.

Larval Biomass and Production

The regression

$$\log(\text{weight}) = 3.37(\log[\text{head width}]) - 0.48 \quad (r^2=0.97,\ n=64)$$

was generated to predict the weight of larvae (mg) based on head capsule width (mm). This regression was based on the dry weights of larvae collected on June 15 and 23, 1982 (the weight of first instar larvae was estimated using the mean weight of the eggs). The regression was used to interpolate

Table I.3 The number of samples (collected on one date from shifting sand areas) containing particular numbers (*N*) of *P. centralis* larvae.

Number of larvae (*N*)	Number of samples with "*N*" larva
0	8
1	6
2	7
3	2
4	0
5	1

the weights of all *P. centralis* larvae collected on particular dates during the study. These weights were in turn used with the mean larval densities (Fig. I.4) to obtain estimates of standing crop (Table I.4).

Production of *P. centralis* larvae in the Sand River were obtained using the instantaneous growth method (Waters and Crawford, 1973; Waters, 1977). The total annual larval production of *P. centralis* was found to be 18.40 and 5.67 $mg/m^2/year$ for 1980 and 1981 respectively. These estimates were relatively low on a per unit area basis, when compared with herbivirous or detritivorous mayflies in other habitats (Waters, 1977).

Larval Behavior

Examination of foregut contents indicated that *P. centralis* larvae preyed primarily on chironomid larvae (*Robackia demeijerei* and *Rheosmittia*) characteristically associated with the sandy habitats of the Sand River. The only other prey items found in the guts of *P. centralis* larvae were small *Baetis* and *Centroptilum* mayfly larvae.

To determine whether *P. centralis* larvae prey more frequently on particular species of chironomids, I examined the frequency of occurrence of chironomid taxa in the guts of three *P. centralis* larvae collected from the SS area June 9, 1981. Table I.5 compares the number in each of three chironomid taxa found in the guts of stage III *P. centralis* larvae with that expected to be found based on the the

Table I.4 Production calculation for *P. centralis* larvae, determined by the instantaneous growth method (G= instantaneous growth rate, <B>= mean standing crop, and P= production).

1980

Date	Density (no./m²)	Mean Wt. (mg)	Standing crop (mg/m²)	G	<B> (mg/m²)	P (mg/m²)
Ma 07	1.72	0.010	0.017			
				1.92	0.06	0.12
Ma 21	1.61	0.068	0.109			
				2.12	0.42	0.90
Jn 05	1.30	0.568	0.738			
				2.37	7.23	17.15
Jn 18	2.25	6.095	13.714			
				0.02	11.52	0.23
Jl 02	1.50	6.221	9.332			
					total	18.40

1981

Ap 23	2.22	0.004	0.009			
				-0.29	0.01	0.00
Ma 07	0.83	0.003	0.002			
				4.18	0.07	0.29
Ma 21	0.69	0.197	0.136			
				2.49	1.35	3.37
Jn 10	1.08	2.379	2.569			
				0.55	3.67	2.01
Jn 23	1.16	4.116	4.775			
					total	5.67

benthic densities of the chironomid taxa in SS areas on June 9, 1981 (Chapter 2). Chi-square goodness-of-fit analysis was used to determine whether there were significant differences ($p<0.05$) between these values. Because of the low numbers expected in the "other chironomids" category, it was necessary to pool this category alternately with the other two categories to use Chi-square analysis. The analysis indicated that the guts of the *P. centralis* larvae consistently contained significantly ($p<0.025$) more *Rheosmittia sp.* larvae, and less *Robackia demeijerei* larvae than would be expected based on the estimated benthic densities of these chironomids. But the apparent selection for *Rheosmittia* larvae by *P. centralis* does not necessarily imply active discrimination; it may only reflect the relative availability of the various species.

In laboratory streams, *P. centralis* larvae foraged principally along the upstream face of actively moving sand dunes. Their long maxillary palpi were extended into the substrate in the same manner as that described for *Analetris eximia* by Lehmkuhl (1976). In the presence of sufficiently high current velocities (high enough to cause significant movement of sand), *P. centralis* larvae exhibited a unique foraging behavior. A larva would, with its anterior end facing the current, rear-up on its prothoracic and mesothoracic legs, bend the head steeply downward, and deflect the flow of water at the surface of the sand. This caused a rapid erosion of the sand in the area beneath the

Table I.5 Abundance of three taxa of chironomid larvae in the guts of three *P. centralis* larvae. The number in brackets is the expected number of chironomid larvae based on the mean benthic densities of these taxa in the shifting sand (SS) area.

Taxa	Larva 1	Larva 2	Larva 3
Rheosmittia sp.	79(71)	49(42)	62(54)
Robackia demeijerei	2(10)	0(6)	0(7)
other chironomids	2(2)	0(1)	0(1)

front margin of the head and presumably exposed chironomid larvae. The *P. centralis* larva would move slowly backwards along the face of the dune, usually leaving behind a shallow groove, which was rapidly filled by eroding sand. When a chironomid larva was encountered, it was rapidly pulled from the sediment, manipulated by the mouthparts, and engulfed, either head or caudal end first. The rapid consumption (large chironomid larvae being consumed in 1 to 3 seconds) and the presence of intact chironomid larvae in the foregut of *P. centralis* suggest that little mastication occurs.

Pseudiron centralis larvae were also observed to use their heads in a similar manner to aid in avoiding the direct effects of the current. Using its claws to retain a hold on the sediment, a larva would rear-up on all legs and bend the head downward. Water flow was thus deflected downward causing a cavity to be eroded in the sand between the legs. The body was then pulled down by the legs into this shallow cavity. The dorsal surface of the larva was thus made flush with the surface of the substrate, and much of the dislodging effect of the current was probably avoided. In this position, eroding sand grains would roll over the larva, sometimes burying it beneath a thin layer of sand. This behavior was frequently observed after a foraging bout.

Experimental Studies

Experiment 1 The first experiment consisted of a series of pairwise comparisons between seven substrate particle size categories ranging from 0.06 to 6.35 mm (Table I.6). Each of the two substrate types to be compared was placed in two trays with dimensions of 16.0 x 5.5 x 1.6 cm, and these trays were then arranged in a 2 x 2 latin square design. The four trays were then placed in an artifical stream driven by a paddle wheel (Ciborowski, 1982); the stream had a width of 11 cm and a water depth of 14 cm. One stage III larva was placed on the substrate in each of the four trays and the stream was then run at a surface velocity of 12 cm/s for 15 minutes. This velocity was the maximum velocity that could be achieved without significant outwash of the finer substrate particles. After the 15 minutes, the number of larvae on each of the substrates was counted and recorded.

Four replicates were obtained for each pairwise comparison. Data were analyzed for each pairwise comparison, using a two-tailed binomial test (Zar, 1974) to indicate the presence of significant ($p<0.05$) differences between the sum of the four replicates.

Table I.6 indicates, for each particle size class, the total of the four replicates in each pairwise comparison. Particle sizes in the range from 0.063 - 2.00 mm appeared to be the only sizes actively chosen by larvae of *P. centralis*. When larvae were given the choice between the two coarsest

Table I.6 Number of *P. centralis* larvae on each substrate in pairwise comparisons of seven different particle size categories: I (0.06-0.12 mm), II (0.12-0.25 mm), III (0.25-0.50 mm), IV (0.50-1.00 mm), V (1.00-2.00 mm), VI (2.00-3.36 mm), and VII (3.36-6.35 mm). Asterisk indicates significantly different pairs (binomial test, $p<0.05$).

Particle Size Category	I	II	III	IV	V	VI	VII
I	-	7	9	12	9	15*	16*
II	9	-	10	13*	12	16*	16*
III	7	6	-	9	14*	14*	16*
IV	4	3*	7	-	10	15*	16*
V	7	4	1*	6	-	11	15*
VI	1*	0*	2*	1*	3	-	5
VII	0*	0*	0*	0*	1*	1	-

particle size classes (2.00-3.36 and 3.36-6.35 mm), 10 of the 16 larvae left the substrate and drifted in the water column after spending only a short time on the substrate. In contrast, the highest number of larvae drifting in all the other comparisons was two.

Although discrimination was exhibited between substrates of nonadjacent size classes, no significant discrimination was exhibited between adjacent classes. This suggests that if the experiment had been designed only to compare adjacent classes then no significant selection would have been exhibited.

Experiment 2 To clarify some of the ambiguity of the first experiment, a second experiment was undertaken. The second experiment tested for selection amongst four substrate size categories simultaneously. Each category was placed in four plexiglas trays (6.0 x 6.0 x 2.3 cm), which were randomized within a 4 x 4 arrangement with the constraints that no substrate category occurred more than once in any column or row and all substrate categories contacted all other substrate categories the same number of times (Plate I.2). Two runs were conducted, the first utilizing the substrate size categories 0.06 - 0.12, 0.12 - 0.25, 0.25 - 0.50, and 0.50 - 1.00 mm; and the second using the categories 0.25 - 0.50, 0.50 - 1.00, 1.00 - 2.00, and 2.00 - 3.36 mm. One stage III larva was placed on the substrate in each of the 16 trays, and the number of larvae on each of the substrate

Plate I.2 Apparatus used in the second experiment to examine substrate selection in *Pseudiron centralis* larvae.

types was counted after one hour. Each run consisted of four replicates, all carried out in an air-powered recirculating stream having a width of 30 cm, a depth of 7 cm, and a mean velocity of 12 cm/s.

Results are presented in Table I.7. A chi-square goodness-of-fit test was used to analyze each of the runs separately.

The first run of this experiment examined substrate selection for the four categories from 0.06 to 1.00 mm. The chi-square value was 15.19, indicating significant differences ($p<0.005$) between the four categories. Subdivision of the chi-square analysis (Zar, 1974) indicated that the two smallest size categories (0.06-0.12 and 0.12-0.25 mm) were selected significantly ($p<0.05$) more often than were the two larger categories (0.25-0.50 and 0.50-1.00 mm). In the second run, the chi-square value was 38.96 indicating highly significant differences ($p<0.001$) between the categories. Subdivision of the chi-square analysis further indicated that particle sizes from 0.25 to 1.00 mm were selected significantly more often ($p<0.05$) than particle sizes from 1.00 to 3.36 mm.

The results of the two experiments indicate that *P. centralis* larvae select most frequently for fine to medium sands (0.06-1.00), selecting coarse sand (1.00-2.00 mm) less often, and generally avoiding substrates with particle sizes greater than 2.00 mm.

Table I.7 The total number of larvae on each substrate type in each run of Experiment 2.

Particle Size Category (mm)	Total Number of Larvae on Each Category	
	First Run	Second Run
0.06-0.12	25	-
0.12-0.25	14	-
0.25-0.50	8	23
0.50-1.00	7	29
1.00-2.00	-	6
2.00-3.36	-	0

Experiment 3 A third experiment was conducted to determine whether *P. centralis* larvae discriminate between fine sand (particle size 0.06 - 0.12 mm) and silt (particle size <0.06 mm). Four trays (11.5 x 11.5 x 3.0 cm), two containing fine sand and two containing silt, were arranged in a 2 x 2 latin square. Two larvae were placed on the substrate in each tray. After one hour, the number of larvae on each of the two substrate types was recorded. There were four replicates. This experiment was run in the absence of current (a highly artificial situation for *P. centralis* larvae), since even the lowest detectable water velocities caused some outwash of silt. Results of the four replicates of this experiment were summed to yield counts of 17 and 14 for the fine sand and the silt categories respectively. Chi-square analysis of these data indicated no significant ($\chi^2=0.32$, $p>0.50$) discrimination between the two substrates. This lack of discrimination was surprising, because *P. centralis* larvae seem to discriminate strongly against silt areas in the Sand River.

Experiment 4 The spacing behavior of *P. centralis* larvae was examined experimentally to determine: (1) whether the field densities and the random dispersion pattern exhibited by these larvae might be largely due to interactions between individuals; and (2) whether interaction between individuals may have affected the results of the substrate selection experiments. If *P. centralis* larvae actively space, then, as

numbers increase for a limited amount of optimal substrate, the mean density on that substrate should approach an asymptote with extra individuals being displaced either into the drift or to less optimal substrates.

Four trays (6.0 x 6.0 x 2.3 cm) containing sand (particle size 0.25 to 1.00 mm) were placed side by side in an air-powered flow tank with a velocity of 16 cm/s and a depth of 7 cm. Eight larvae were introduced upstream of the substrate trays. After one hour, the number in each tray was counted and recorded. Another four larvae were then introduced and the number on each substrate type was counted again after one hour. This process was repeated until 28 larvae had been introduced into the flow tank.

The results of the experiment are presented in Figure I.5. There was no apparent tendency toward an asymptote, except at the highest larval density used in the experiment, where there was almost no unoccupied space left in the substrate trays.

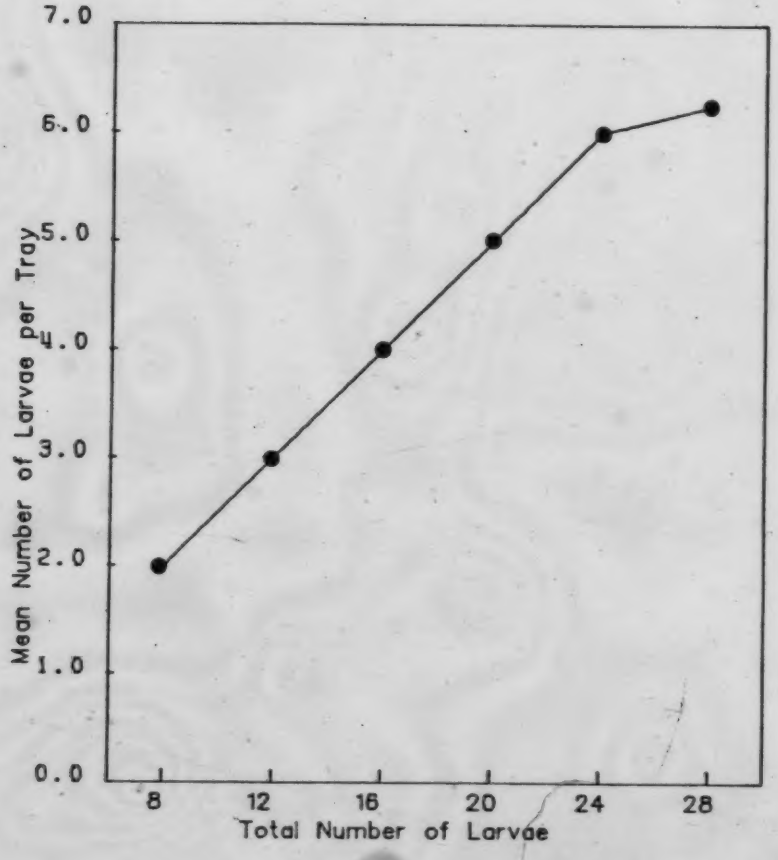

Figure I.5 The mean number of *P. centralis* larvae per tray, as a function of larval density in the experimental tank.

DISCUSSION

Life History Features

In the Sand River, *P. centralis* exhibits a summer type life cycle, with a relatively short larval period and a long egg dormancy (approximately 9 months). Overwintering as a dormant egg appears to be a relatively common strategy in Ephemeroptera (Clifford, 1982). Long egg dormancies have been reported for *Dolania americana* (Harvey *et al.*, 1980), and have been suggested for *Analetris eximia* Edmunds (Lehmkuhl, 1976), both of which are predaceous mayflies associated with sandy river beds.

Clifford (1982) indicates that the adaptive significance of the summer cycle has generally been attributed to the avoidance of harsh or uncertain conditions during winter, but suggests that this life cycle may be an adaptation to shorten the larval period and thereby minimize the impact of such factors as predation on this stage.

Pseudiron centralis larvae did not seem to exhibit high mortality rates, based on the changes in larval density over time (Fig. I.4). Also the relatively low fecundity of females does not suggest high levels of larval or egg mortality. Thus it seems unlikely that the adaptive significance of the life cycle pattern of *P. centralis* is to minimize larval mortality.

It is apparent that the density of psammophilous chironomid larvae remains high throughout the year (see

Chapter 2 and 3). Since *P. centralis* was the only macroinvertebrate predator collected on shifting sand areas in the Sand River, it appears that the chironomid populations of this habitat remain unexploited for much of the year. Given the presence of a relatively constant availability of prey items, the *P. centralis* population, would be expected to exhibit a more staggered larval growth and emergence pattern. The absence of this pattern suggests some overriding factor makes developmental synchrony advantageous to members of this population.

The large size of *P. centralis* eggs was probably not simply a function of the duration of the dormancy period and the food requirements of the embryo, since most other Ephemeroptera with similar egg dormancy periods do not possess such large eggs. *Pseudiron centralis* larvae may be large at hatching because of their predaceous habits (chironomid larvae were found in the guts of even the smallest stage I larvae examined), which may impose a minimum size constraint, below which larvae cannot prey effectively on chironomids. Alternately, *P. centralis* larvae might be constrained to a certain minimum size to cope effectively with the dynamic nature of the sandy beds on which they are found.

Larval Habitat Associations

The shift in habitat association exhibited by *P. centralis* during larval development may in part also be a

reflection of the dynamic nature of sandy river beds. *Pseudiron centralis* larvae occupy the surface of the substrate; thus they are exposed to the current and any substrate movements that occur. Given the high current velocities, turbulence, and active movement of substrate that characterize shifting sand areas in the mainstream of the Sand River, it seems reasonable that stage I larvae cannot cope with these stresses and are thus confined to marginal areas. However, the almost exclusive association of stage III and IV larvae with areas of shifting sand is more difficult to explain.

In the laboratory, stage III and IV *P. centralis* larvae were able to survive for long periods at low current velocities, and one larva survived for a week in the absence of significant current. It thus seems unlikely that there is an immediate physiological necessity to seek out areas with relatively high current velocities, such as found over shifting sand substrates.

Results of the substrate selection experiments provide a possible explanation for the absence of stage III and IV larvae from gravelly sand areas of the river bed, since they indicated that *P. centralis* larvae avoid gravel. However, there is no indication as to why stage III and IV larvae were absent from marginal sand areas.

Two hypotheses are advanced to account for the observed distribution pattern of stage III and IV *P. centralis* larvae in the Sand River: (1)predator or competitor pressure is

lower in areas of shifting sands; or (2)food availability (i.e. chironomid larvae) is greater in shifting sands.

Pseudiron centralis larvae are the only epibenthic macroinvertebrates occupying shifting sand areas in the Sand River, and they are much larger than any other macroinvertebrate in this habitat. Possibly by occupying this area, they avoid interactions with the much more diverse epibenthic fauna of gravelly sand and marginal sand areas. Prominent macroinvertebrates associated with GS and MS areas in the Sand River are the larvae of the family Gomphidae (Odonata). These predaceous dragonfly larvae have been suggested to be partially responsible for restricting the distribution of *Dolania americana* larvae to shifting sand areas through competition for food resources (Tsui and Hubbard, 1979). For *P. centralis* larvae, predation by odonates is probably more important as a determinant of distribution than is competition for food resources. This is suggested by the rapid decline in the numbers of *P. centralis* larvae in laboratory streams that contained gomphid larvae. It is possible that an active foraging strategy, such as that exhibited by *P. centralis* larvae, is incompatible with the presence of a significant number of 'sit-and-wait' predators, such as gomphid larvae. However, the susceptibility of *P. centralis* to such predation has not been determined, and I did not measure the gomphid larval density; hence this hypothesis could not be tested.

The second hypothesis predicts a greater prey availability (i.e. chironomid larvae) in shifting sand areas than in other areas examined. Availability is defined here as including both the abundance (numerical and biomass) and the accessibility of chironomid larvae. Chapter 2 reports the mean total density and biomass of larval Chironomidae on the various substrate types in the Sand River for the ice-free season in 1981. Considering only the sampling intervals when stage III and IV *P. centralis* larvae were likely present (Fig. I.2), ANOVA indicated no significant differences in mean density ($F=0.922$, $p=0.40$) or biomass ($F=0.388$, $p=0.68$) of chironomid larvae in the three types of substrate. This suggests that *P. centralis* larvae occupying shifting sand areas gained no apparent advantage in terms of food abundance.

The relative accessibility of chironomid larvae in the various substrates types was not determined, but the observed preference of *P. centralis* larvae for the eroding upstream face of sand dunes suggests that the movement of the sand may expose chironomid larvae. Since *P. centralis* larvae have not been observed to burrow actively after prey, except in the manner described previously, it is possible that *P. centralis* may exploit prey items exposed by the action of the current and the instability of the substrate in shifting sand areas.

A complicating factor is that changes also occur in the composition of the chironomid communities associated with

the substrate types. Shifting sands are dominated almost exclusively by chironomid larvae that live in the interstices between sand grains (Chapter 2); whereas marginal sand and gravelly sand areas support large numbers of tube-dwelling and burrowing forms. The numerically dominant species in shifting sand areas was also *Rheosmittia sp.*, which appeared to be a favoured prey item of *P. centralis* larvae (Table I.5). This is unlikely, however, to explain the exclusive association of stage III and IV *P. centralis* larvae observed, since *Rheosmittia sp.* larvae also occurred in substantial numbers in marginal sand areas (Chapter 2).

Larval Dispersion and Spacing Behavior

The random dispersion pattern of stage III and IV *P. centralis* larvae on shifting sand areas greatly facilitated accurate population estimates. Random dispersion patterns have seldom been reported for lotic benthic invertebrates, although they have been found in populations of species frequenting areas of relatively uniform substrate composition (Resh, 1979). The presence of a random dispersion pattern on shifting sands suggests *P. centralis* larvae might be perceiving this area as a relatively uniform patch, at least at the population level; and supports the designation of shifting sand areas as a distinctive habitat for *P. centralis*.

Observations suggest that *P. centralis* larvae will not tolerate physical contact with other individuals. Such contact elicits a response whereby one or both individuals will rapidly swim or crawl away. The spacing experiment indicated that *P. centralis* larvae seem to tolerate a mean density of about six individuals in a 36 cm^2 area. This density could have easily been accommodated in the substrates used in the substrate selection experiments, and thus it is unlikely that spacing of individuals had an appreciable effect on these experiments. Since the density tolerated by larvae in the spacing experiment corresponds to a density of 1600 individuals/m^2, it seems unlikely that spacing is an important determinant of field densities, even given that actively foraging individuals would probably only tolerate a much lower density.

CONCLUSIONS

Although *P. centralis* larvae and adults are rarely collected, the species is probably not rare. The low densities at which *P. centralis* occurs and the difficulties of sampling the invertebrate fauna near and in the mainstream of larger rivers have probably combined to give this impression. This is probably true for the genus *Pseudiron* as a whole. Specimens of *Pseudiron* have been collected in sandy reaches of all major river systems in North America, with the exception of the St. Lawrence River and some drainages west of the Rocky Mountains.

Barton (1980) commented on the generalized invertebrate assemblages associated with the sandy beds of larger rivers over wide geographic areas. Mayflies of the genus *Pseudiron* appear to be consistent members of these assemblages in North America.

In the Sand River, and probably in other rivers, *Pseudiron* larvae are the only epibenthic invertebrate predators that occupy areas of actively shifting sand. They are highly specialized predators on the chironomid fauna of these areas, and as such may play an important role in the biological communities associated with shifting sand areas. Further examination of the biology and ecology of *Pseudiron* is likely to increase our understanding of one of the dominant habitat types in river ecosystems.

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II. THE LIFE HISTORY AND ECOLOGY OF *Robackia demeijerei* Krus. AND *Rheosmittia sp.*, TWO RIVERINE CHIRONOMIDAE (DIPTERA) ASSOCIATED WITH SHIFTING SAND SUBSTRATES IN RIVERS.

ABSTRACT

Chironomid larvae are often the dominant macroinvertebrates associated with areas of actively shifting sand in the beds of larger rivers. This study examines the ecology of *Robackia demeijerei* and an undescribed species of *Rheosmittia* in a river in central Alberta, Canada. *Robackia demeijerei* was univoltine with an extended emergence pattern. *Rheosmittia sp.* exhibited a bivoltine life cycle with well defined emergence periods. Larval densities of both species were highest where the sand was in active motion. Most larvae occurred in the upper 10 cm of substrate. Larvae of neither species constructed tubes or tunnels in the substrate. The small cross-sectional diameters of these larvae suggest that they are true interstitial forms, using the space between sand grains. Laboratory experiments indicated that larvae of both species select substrates in the range of 0.50-2.00 mm. This was consistent with model predictions of accessibility and suitability of interstitial space for vermiform animals of given cross-sectional diameters. Separation of substrate types, using visual and tactile criteria, predicted the abundance of larvae of both species more accurately than the particle size distributions of the substrates. There was no clear relationship between depth of the oxidized layer in the sediments and larval abundance. A negative relationship existed between abundance of larvae of other chironomids, and those of *R. demeijerei* and *Rheosmittia sp.*.

INTRODUCTION

Chironomid larvae appear to be the dominant macroinvertebrates occupying areas of unstable shifting sand in the beds of most large rivers (Berner, 1951; Zhadin and Gerd, 1961; Barton and Lock, 1979; Barton, 1980; Seagle et al. 1982), although Oligochaeta sometimes achieve dominance in heavily polluted systems (Zhadin and Gerd, 1961). The chironomid fauna of sandy river beds appears to be a highly generalized assemblage of species, some occurring over wide geographic and climatic ranges (Saether, 1977; Barton, 1980). This fauna has seldom been studied except in the course of general taxonomic or ecological surveys.

Robackia demeijerei (Kruseman) is a widely distributed species in the subfamily Chironominae, occurring in most larger rivers in North America, some rivers in the U.S.S.R., and in the beaches of some lakes in North America (Saether, 1977). Barton (1980) indicated that larval *R. demeijerei* were chacteristically associated with coarse sand in the Athabasca River. Zhadin and Gerd (1961) suggest that members of the group to which the genus *Robackia* belongs are all predaceous.

Rheosmittia sp. is an undescribed species in the subfamily Orthocladiinae and was referred to as "Orthocladiinae B" by Barton (1980) and Barton and Lock (1979) (D.R. Oliver pers. comm.). Barton (1980) suggests that this species is probably widespread but has been overlooked because of its small size. The genus is known

from Europe and North America and until recently was included in the genus *Eukiefferella* (D.R. Oliver pers. comm.)

My study examines the life history, distribution, abundance, and behavior of *R. demeljerei* and *Rheosmittia* in the sandy substrates of a medium-sized river in central Alberta.

STUDY SITE

The study was carried out at the mouth of the Sand River (54°23' N, 111°2' W), located in east-central Alberta. Above its mouth, the Sand River is approximately 30 m wide with mean thalweg current velocities ranging from 60-150 cm/s. The mean annual discharge over the study period was approximately 16 m^3/s. The bottom of the Sand River is composed almost exclusively of sand, with silty areas occurring near the banks and with an occasional gravel bar occupying part of the bed. The mean daily summer temperature (June to September) of the Sand River was approximately 20°C. A more detailed description of the study area is given in Chapter 1.

METHODS

Four substrate types were recognized in the bed of the Sand River: silt (SI), marginal sand (MS), gravelly sand (GS), and shifting sand (SS). These substrates were defined by a series of visual and tactile criteria (Table II.1).

Table II.1 Criteria for identifying the four major substrate types in the Sand River.

Substrate Category	Visual and Tactile Criteria
Silt (SI)	soft sticky texture, abundant visible silt, dark grey or black color
Marginal Sand (MS)	firm fine-grained texture, some visible silt, few sand particles in active motion
Gravelly Sand (GS)	firm coarse texture, abundant gravel apparent, few sand particles in active motion
Shifting Sand (SS)	soft loose texture, no apparent silt, actively moving sand dunes

Samples were obtained along ten transects, set out at 5 m intervals along a 50 m stretch near the mouth of the Sand River. Samples were obtained at intervals determined by the occurrence of the various substrate types along each transect (silt areas were not sampled). Samples were obtained from the middle area of those substrates that occurred in narrow bands parallel with the banks (MS and GS) and at intervals of 5,10,20, and 30 m from the east bank, wherever possible in SS areas. A series of samples was obtained prior to freeze-up in 1980 (November 9) and on a roughly bi-weekly basis during the ice-free season of 1981 (April 23 to October 28). Additional samples were obtained on June 23, 1982.

The principal sampling device was a modified version (see Appendix 1) of the core-freezer described by Shapiro (1958). A handled Surber sampler (mesh size 0.243 mm) was used exclusively on Nov. 9, 1980 and, in conjunction with the core-freezer, on May 7,1981.

Cores were obtained by pushing the corer into the sediments to a depth of 25 cm, and then pouring a mixture of dry ice and iso-butyl alcohol into the outer jacket of the sampler. After approximately 5 minutes the corer was removed from the sediments and transported to the river bank, where the dry ice butanol mixture was poured from the outer jacket. If the core was to be kept intact, the water column over the core was poured off into a labelled container, water was poured into the outer jacket, and the intact core

would fall out into another container. If the core was not to be kept intact, then the core and water column were collected into one container. All samples were frozen in the field and stored at -28°C until examination.

Samples were obtained with the Surber sampler by disturbing the 930 cm^2 area defined by the sampler, with the foot for 30 seconds. This technique disturbed the substrate down to a level of approximately 10 cm. Samples were placed in jars and preserved in 95% ethanol until examination.

In the laboratory, samples were thawed where necessary and the organic material in the samples was separated from inorganic by elutriation. The organic material was examined under a dissecting microscope at 12X, and all organisms were removed, identified, and counted. For the cores, the organic material remaining after all organisms were removed was returned to the inorganic fraction, and then the entire sample was air-dried.

Larvae of *R. demeijerei* and *Rheosmittia sp.* were separated by instar and the number in each of the various instars was recorded. Instar was determined by head capsule length, which was measured from the hind lateral margin of the head to the base of the mandibles. Head capsule width was obtained from the widest part of the head (approximately at the level of the eyes) in both species. All measurements were obtained using an eyepiece micrometer, either under a dissecting microscope at 100X or under a compound microscope at 200X.

To determine the vertical distribution of *R. demeijerei* and *Rheosmittia sp.* larvae, cores that had been collected intact were cut into 5 cm sections. Each of these sections was then treated as an individual sample and the number of larvae in each section recorded.

To determine the mean weight of each discernible larval instar, larvae removed from the cores were dried at 60°C for 24 hours and weighed on a microbalance to the nearest 0.002 mg. Because of the minute size of the early instar larvae, it was necessary to weigh individuals as groups (Table II.3).

The gut contents of larvae were qualitatively examined in slide mounted specimens that were squashed to spread the material in the guts. Uncleared specimens and specimens cleared in 10% potassium hydroxide for 24 hrs at room temperature were examined under a compound microscope at a series of magnifications (100-400X).

The particle size distribution of the substrate types in terms of weight was determined for samples obtained from two dates (June 9 and August 5, 1981). These samples were dried for 24 hrs at 60°C, and dry sieved (for 7 minutes using a mechanical sieve shaker) through a series of eight brass sieves (mesh sizes: 12.70, 3.36, 2.00, 1.00, 0.50, 0.25, 0.12 and 0.06 mm) to yield nine particle size classes. The material in each fraction was then weighed to the nearest 0.1 mg.

RESULTS AND DISCUSSION

Life Histories

Table II.2 shows the mean head capsule lengths and widths for all larval instars of *R. demeijerei* and all distinguishable larval instars of *Rheosmittia sp.*. First and second instar *Rheosmittia sp.* larvae were not separable by head width or head length and were treated together.

The mean dry weight of each discernible larval instar of the two species is given in Table II.3. *Robackia demeijerei* and especially *Rheosmittia sp.* are relatively small chironomids both in terms of larval head capsule dimensions and larval dry weight.

Figure II.1 illustrates the relative proportion of individual instars for both species in the Sand River during the study. *Rheosmittia sp.* appears to exhibit a bivoltine life cycle in the Sand River, with a winter and a summer generation. After overwintering as third instar larvae, *Rheosmittia sp.* larvae develop rapidly in the spring and appear to pupate and emerge as adults in late May. Eggs laid by the adults of this winter generation hatch after a short time, and large numbers of first and second instar larvae appear in early June. Larvae in this summer generation then develop over a 6 to 8 week period, pupating and emerging in late July and early August. Larvae of the next winter generation first appear in early August and develop as far as the third larval instar before freeze-up, at which time

Table II.2 Mean head capsule lengths and widths for each discernible larval instar of *Robackia demejerei* and *Rheosmittia sp.*.

Robackia demeijerei

Instar	Mean Head Length (μm) [S.E.]	n	Mean Head Width (μm) [S.E.]	n
I	69[2]	10	52[2]	10
II	98[1]	14	64[1]	14
III	134[1]	15	87[1]	15
IV	194[1]	14	130[1]	14

Rheosmittia sp.

I+II	55[2]	14	47[1]	11
III	74[1]	4	61[1]	4
IV	91[2]	6	80[1]	6

Table II.3 Mean dry weight of all distinguishable larval instars of *Robackia demeijerei* and *Rheosmittia sp.*. Also indicated is the number of larvae weighed per sample, and the number of samples weighed to determine the mean.

Robackia demeijerei

Instar	no./sample	no. samples	mean wt. (μg)	S.E.
I	10	7	1.5	0.7
II	5	51	3.5	1.2
III	1	104	12.6	5.3
IV	1	57	29.1	13.2

Rheosmittia sp.

I+II	20	45	0.7	0.3
III	10	53	1.7	0.8
IV	5	44	7.2	2.8
V	5	5	7.6	1.5

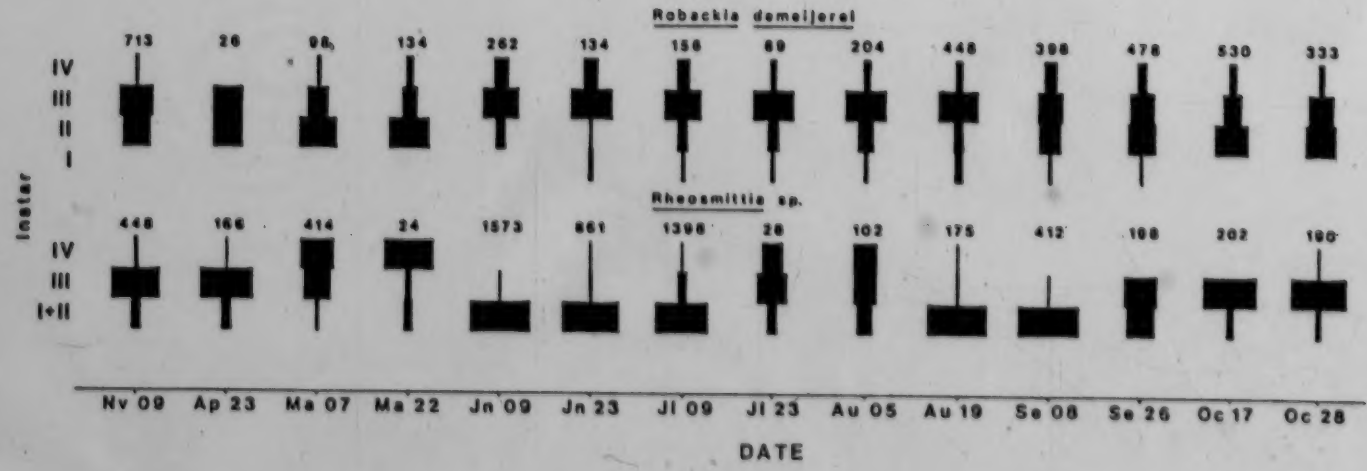

Figure II.1 Relative frequency of discernible larval instars of *Robackia demeijerei* and *Rheosmittia sp.* over the study period.

development seems to cease until spring.

The life cycle of *R. demeijerei* (Fig. II.1) in the Sand River is difficult to interpret because both emergence and hatching appear to occur over an extended period. A comparison between the life cycle exhibited in Figure II.1 and the density of *R. demeijerei* larvae during this study (Fig. II.2) suggests that this species is univoltine in the Sand River. First instar larvae appear from late June until late September, with maximum numbers occurring in late August. The low number of first instar larvae was probably a function of either a relatively short time spent in this stage or reflects utilization of a different habitat by first instar larvae; both are common strategies exhibited by other chironomids (Oliver, 1971). Larvae develop throughout the summer and fall, with most individuals achieving second or third instar before freeze-up. Overwintering can occur in either second and third instar and probably is a major factor contributing to the difficulty of interpreting the life cycle of this species in the Sand River. Development appears to stop during winter, but resumes after the break-up of ice in spring. The presence of first and fourth instar larvae suggests that adult emergence and egg laying take place over an extended period, probably from the end of May to the end of September. Since *R. demeijerei* pupae were seldom encountered, it is likely that individuals leave the substrate after pupation.

Larval Density and Distribution

The densities of *R. demeijerei* and *Rheosmittia sp.* on the three substrate types are presented in Figures II.2 and II.3. The values obtained for Nov. 9, 1980, were based on estimates obtained with a Surber sampler and have been corrected for the relative efficiency of this type of sampler when compared with the freeze-corer. This correction factor was determined from the comparison of the density estimates obtained from six pairs of Surber and core-freezer samples taken in close proximity in the SS area on May 7,1981. The efficiency of the Surber sampler was found to be approximately 5% (s^2=11.6) for *Rheosmittia sp.* and 13% (s^2=118.8) for *R. demeijerei*. These are likely maximal estimates of sampling efficiency since early instar larvae were not present on this date (Fig. II.1).

To determine whether significant differences existed between the densities of *R. demeijerei* and *Rheosmittia sp.* larvae on the three different types of substrate sampled, one-way analysis of variance (ANOVA) was conducted on log(n+1) transformed data from all dates where all substrate categories were sampled. The probabilities obtained from these ANOVAs (Table II.4) were then pooled (Sokal and Rolhf, 1969) to obtain an overall probability. This analysis indicated that significant differences existed between the densities of each species in the three substrate types (χ^2=38.36, $p<0.01$ for *R. demeijerei*; and χ^2=68.72, $p<0.001$ for *Rheosmittia sp.*).

Table II.4 Value of 'F' ratio and the probability (p) of this value from ANOVAs calculated for *Robackia demeijerei* and *Rheosmittia sp.* on 10 dates in 1981.

	Robackia demeijerei		*Rheosmittia sp.*	
Date	F	p	F	p
Ma 07	1.586	0.242	0.516	0.608
Ma 22	2.299	0.131	0.504	0.202
Jn 09	0.928	0.408	5.261	0.012
Jn 23	1.543	0.248	0.216	0.808
JI 09	1.488	0.247	3.877	0.035
Au 05	0.611	0.552	9.190	0.001
Au 19	1.162	0.330	4.012	0.031
Se 08	2.186	0.147	5.079	0.021
Se 26	4.640	0.020	10.649	0.001
Oc 17	5.665	0.011	3.629	0.044

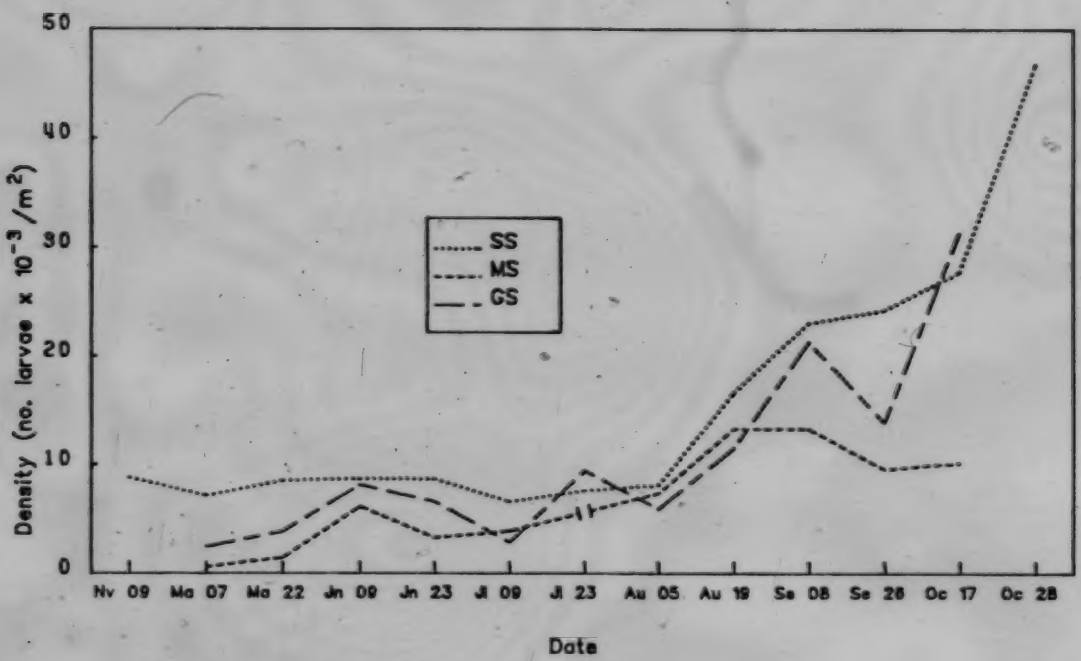

Figure II.2 Mean larval density of *Robackia demeijerei* on the three substate types (SS is shifting sands, MS is marginal sands, and GS is gravelly sand).

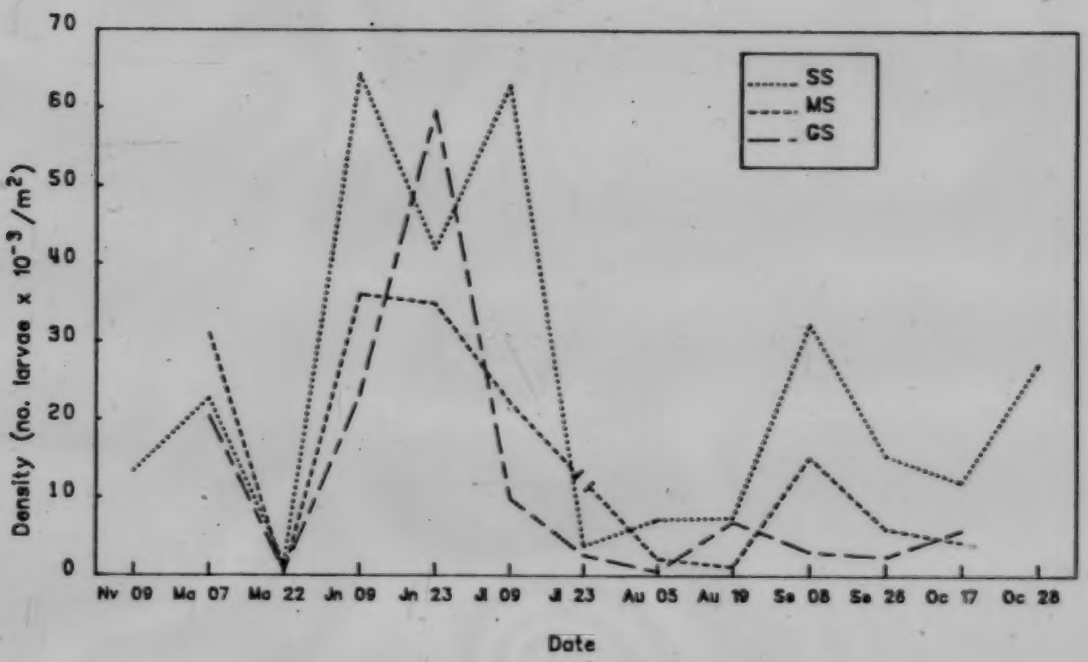

Figure II.3 Mean larval density of *Rheosmittia sp.* on the three substate types (SS is shifting sands, MS is marginal sands, and GS is gravelly sand).

One-way ANOVAs conducted on an overall pooling of log(n+1) transformed data from all dates for each species and each substrate type yielded a similar result (F=8.74 and F=21.53 for *R. demeijerei* and *Rheosmittia sp.* respectively, $p<0.0001$ in both cases), indicating significant differences between the densities of each species in the three substrate types. Duncan's multiple range test (DMR) (Sokal and Rohlf, 1969) indicated that SS areas supported significantly higher ($p<0.05$) densities of both *R. demeijerei* and *Rheosmittia sp.* than did MS or GS areas.

Most (mean=77.4%, S.D.=11.6, n=7) *R. demeijerei* and *Rheosmittia sp.* larvae were found in the upper 10 cm of substrate; however, a few larvae were collected deeper than 15 cm (mean=2.4%, S.D.=4.6, n=7). This is somewhat deeper than reported depths for chironomid larvae in stream muds (Ford, 1962), but is shallower than those reported for coarser substrates (Williams and Hynes, 1974). The results of this analysis of vertical distribution should be viewed as tentative, since the core-freezer freezes the sample from the bottom up; and the chironomids may have moved toward the surface to escape this freezing.

The mean total biomass (mg/m^2 dry weight) for each species on the various substrate types over the year is illustrated in Figures II.4 and II.5. Biomass was determined by indirectly assessing the weight of individuals in each sample from the mean weights (Table II.3) of the different larval instars. Total biomass for each sample was the sum of

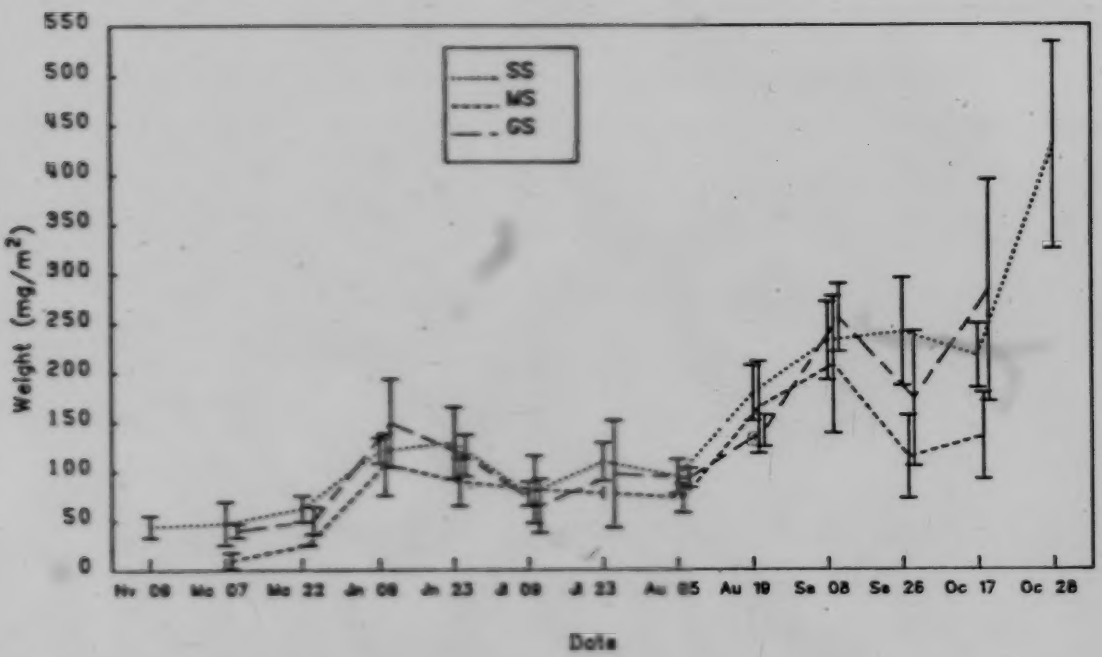

Figure II.4 Mean dry weight (±S.E.) of larval *Robackia demeijerei* on the three substrate types.

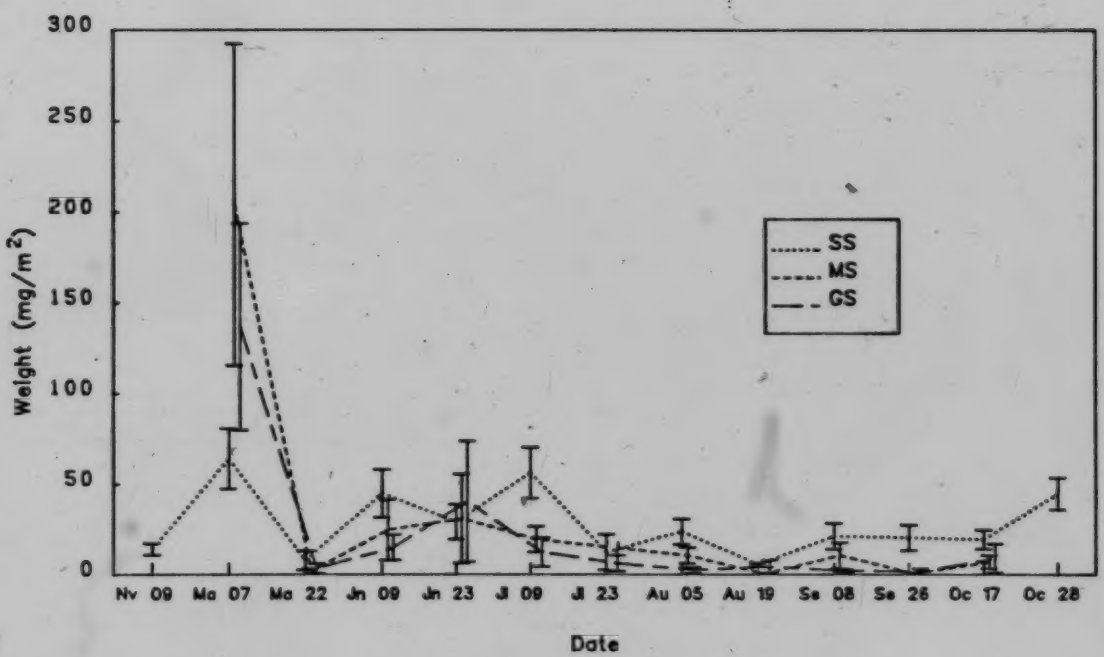

Figure II.5 Mean dry weight (±S.E.) of larval *Rheosmittia sp.* on the three substrate types.

these individual estimates. These data show trends similar to those indicated by the density estimates.

Larval Behavior

The trophic relations of the two species could only be assessed qualitatively, given the technique used to examine the gut contents. The guts of *Rheosmittia sp.* larvae were tightly packed with diatoms, suggesting that these larvae directly exploit sources of primary production in the river bed. The guts of *R. demeijerei* larvae, although containing some diatoms were mostly filled with an unidentifiable amorphous material. Since many predaceous chironomids do not consume the hard parts of their prey (Oliver, 1971), it was impossible to determine whether this material was animal tissue or detritus.

Robackia demeijerei and *Rheosmittia sp.* larvae are similar behaviorally and to some extent morphologically. In the laboratory larvae of neither species constructed tubes, and there was no evidence that burrows were actively maintained. The larvae of these species probably exploit the interstitial space available between sand grains.

When individuals of either species were placed on the surface of sand sediments or were disturbed, they tended to respond by producing copious quantities of a sticky silk, which they attached to nearby sand grains through a vigorous thrashing motion of the head and body. Similar behavior has been described for other species of sand-dwelling

chironomids; Wiley (1980) suggested that this action allows the animal to maintain its position while penetrating the sediment.

Robackia demeijerei larvae exhibit a relatively elongated (fourth instar larvae: body width approximately 0.14 mm, body length approximately 5.8 mm) body form that is somewhat atypical for a chironomid; they superficially resemble larvae of Ceratopogonidae (Diptera). Larvae of *Rheosmittia sp.* though somewhat stouter relative to body width (fourth instar larvae: body width approximately 0.10 mm, body length approximately 2.2 mm), are also relatively more slender than larvae of most other chironomid species.

Substrate Selection Experiments

Experiments were conducted to determine whether *R. demeijerei* and *Rheosmittia sp.* larvae would select substrates with particular particle size distributions. The design consisted of sixteen (2.7x2.7x2.9 cm) substrate cages arranged in a 4x4 matrix inside a 11.8x11.8x3.1 cm tray (Plate II.1). Each cage consisted of a bottom plate made of a 2.7x2.7x0.3 cm piece of plexiglas, and four (0.3x0.3 cm) supports with 0.15 mm mesh nylon netting between them. The 0.15 mm netting allowed free passage of even the largest individuals between cages, while minimizing any leakage of fine particles if the cage was not unduly disturbed.

The cages were filled with one of four substrate size classes: <0.12, 0.12-0.50, 0.50-2.00,and 2.00-6.35 mm. Each

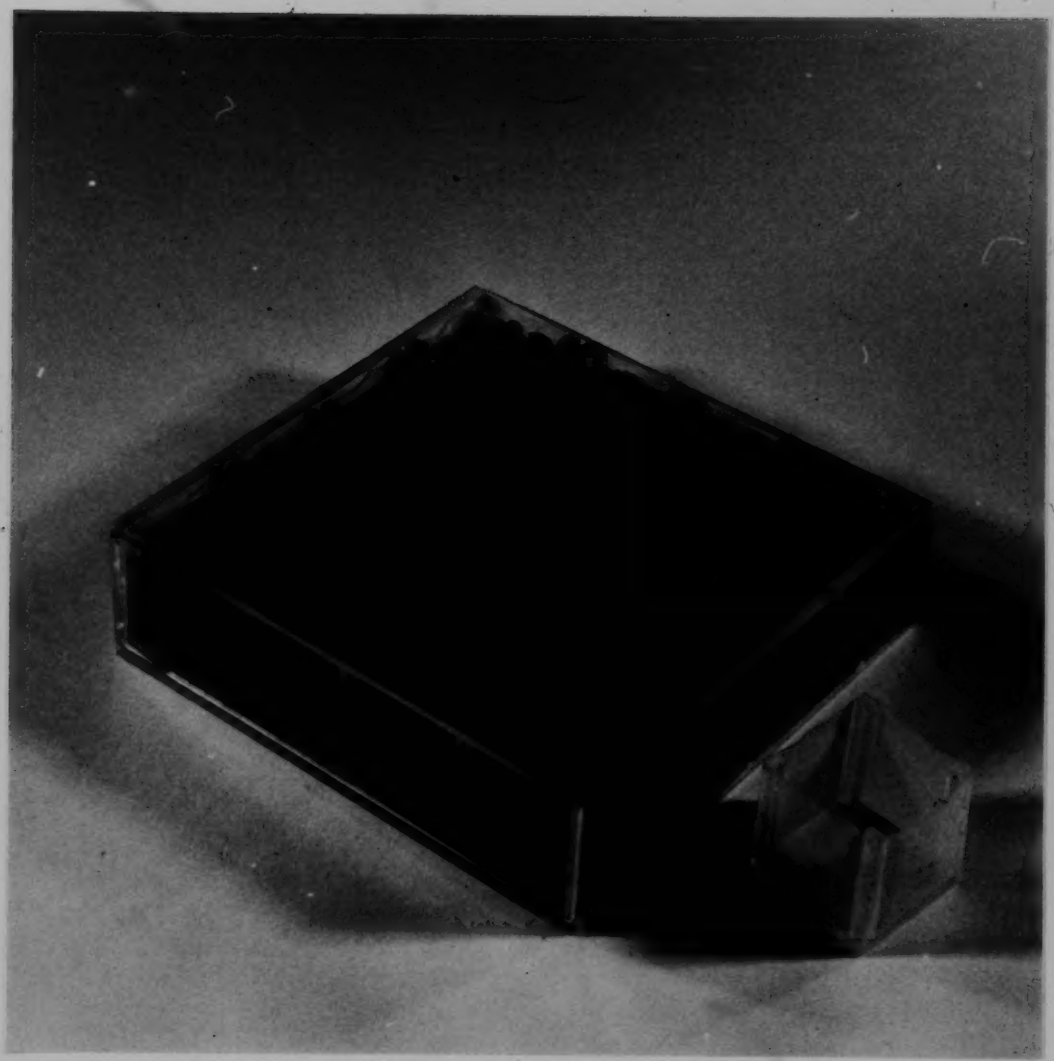

Plate II.1 Experiment apparatus used to test for substrate selection in fourth instar *Robackia demeijerei* and *Rheosmittia* larvae. In the foreground is one of the substrate cages (see text).

of these substrates was made up of equal volumes of particles from two size classes; hence the median particle size in each substrate was easily calculated.

Cage position was randomized in the tray with no substrate class occurring more than once in any row or column, and every substrate type contacting every other substrate type the same number of times within the tray as a whole. The tray was filled with water and ten individuals of the same species were placed on the substrate surface in each cage. Animals were then allowed to burrow into the substrate; after a few minutes, individuals remaining on the surface were buried. The tray was placed in a recirculating artificial stream and exposed to a mean current velocity of 10 cm/s for 24 hours. The tray was then removed and the individual cages placed in separate jars filled with 95% ethanol. The contents of these cages were sorted at 12X magnification under a dissecting microscope and all individuals were removed and counted.

The *R. demeijerei* experiment was repeated three times with different arrangements of the substrates, the *Rheosmittia sp.* experiment was run only once. Fourth instar larvae were used in both experiments.

Results are presented in Table II.5. Only the first run of the *R. demeijerei* experiment is reported since all three runs yielded similar results. The large number of *Rheosmittia sp.* larvae that left the substrate during the experiment was due to pupation (the pupae floated near or at

Table II.5 Mean number and variance of larvae per cage for each substrate category in each of the two experiments. The initial number of larvae per cage was 10.

	Robackia demeijerei		*Rheosmittia sp.*	
Substrate size(mm)	mean no./cage	s^2	mean no./cage	s^2
<0.12	4.50	4.25	1.50	2.25
0.12-0.50	6.75	18.69	4.75	6.19
0.50-2.00	18.00	5.00	8.50	9.00
2.00-6.35	4.75	6.69	2.50	1.25

the water's surface in the artificial stream), and does not represent a normal rate of larval emigration from the sediments into the water column.

The results of the *R. demeijerei* experiment were analyzed using one-way ANOVA; this indicated significant differences ($F=14.25$, $p<0.001$) between the number of larvae on the different substrate types. DMR indicated that the substrate in the 0.50-2.00 mm range was selected significantly ($p<0.05$) more often than all other types of substrate.

One-way ANOVA also indicated significant differences ($F=7.04$, $p<0.01$) in the number of *Rheosmittia sp.* larvae on the four substrates. As in the previous case, DMR indicated that the 0.50-2.00 mm substrate class retained a significantly ($p<0.05$) higher number of larvae than all the other substrates.

Wiley (1981) relates the distribution of some chironomid larvae to their ability to penetrate sediments and the probability of being swept from the substrate before penetration is accomplished. If *Robackia demeijerei* and *Rheosmittia sp.* larvae are interstitial forms, then the volume of accessible interstitial space within the substrate should also be a critical factor in substrate suitability. Crisp and Williams (1971) provide a model for estimating the accessible interstitial space for vermiform animals in relatively homogeneous monomorphic substrates. They estimate that an animal with a cross-sectional diameter equal to 30

to 40% of the grain size would be able to use 50% of the total volume of interstitial space.

By using Crisp and Williams (1971) model and the mean head widths of fourth instar larvae of both species (Table II.2), I calculated the minimum grain size in which 50% of the total interstitial space would be available for the larvae of each species. This analysis indicated that fourth instar *R. demeijerei* larvae would require a particle size greater than 0.32-0.43 mm for more than 50% of the total void space to be available. Fourth instar *Rheosmittia sp.* larvae would require particle sizes greater than 0.20-0.27 mm for access to 50% of interstitial space.

The median particle sizes of the substrates used in the substrate selection experiments were 0.06, 0.25, 1.00, and 3.36 mm respectively. It seems likely that the selection of the 0.50-2.00 mm substrate size class over the finer size classes by fourth instar *R. demeijerei* larvae was influenced by the accessibility of suitable interstitial space in this substrate. There were few individuals in the coarsest substrate class (2.00-3.36 mm), where theoretically the greatest volume of interstitial space should have been available. This might have been due to the difficulty some interstitial animals have in moving through large openings, especially if their bodies do not contact more than a small area of the wall of the opening (Crisp and Williams, 1971).

The association of fourth instar *Rheosmittia sp.* larvae with the 0.50-2.00 mm substrate size class is explained in

much the same manner as that for *R. demeijerei*, except that the 0.12-0.50 substrate size class should also have provided a significant amount of accessible interstitial space for these larvae. Crisp and Williams (1971) point out that fine particles fill the larger interstitial spaces and tend to greatly reduce the accessibility of interstitial spaces. Thus the portion of particles below the median value in the substrates used in my experiments may have decreased the reliability of estimates of the availability of interstitial space based on the median particle size.

The results of these experiments suggest that the distribution of *R. demeijerei* and *Rheosmittia sp.* larvae in the field may have been determined by differences in the distribution of particle sizes in the three substrate types sampled. To determine whether substantial differences existed between the three substrate types, the mean contribution of nine particle size classes to the total weight of the substrate types was measured and pooled for two separate dates (Figures II.6, II.7 and II.8). A Kruskal-Wallis non-parametric ANOVA (Daniel, 1978) was used to determine whether significant ($p<0.05$) differences existed in the weight of material in each individual particle size class among the three substrate types. Dunn's test (Daniel, 1978) was used to assign differences between the substrate types where the previous analysis had indicated significant differences. The use of actual weights rather than proportions was justified, because there were no

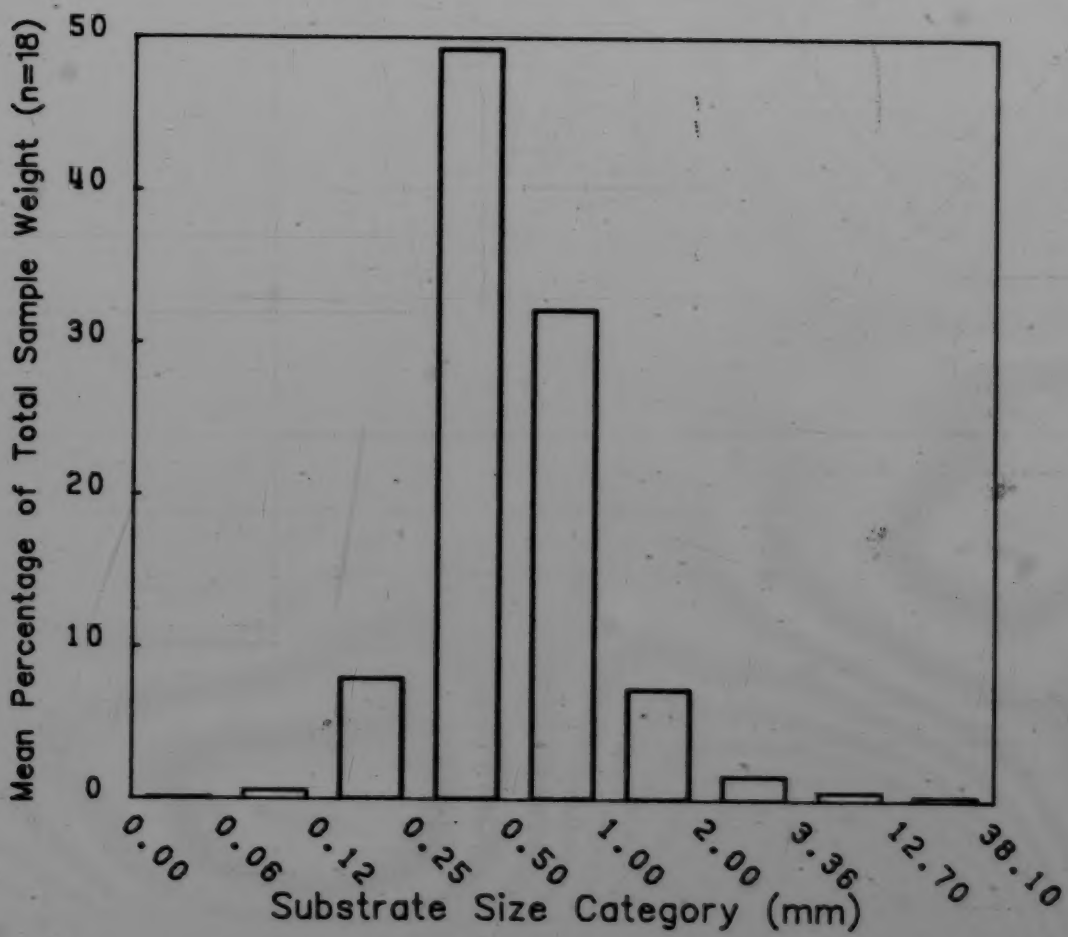

Figure II.6 Mean particle size distribution by weight (g) of substrate from the shifting sand (SS) area.

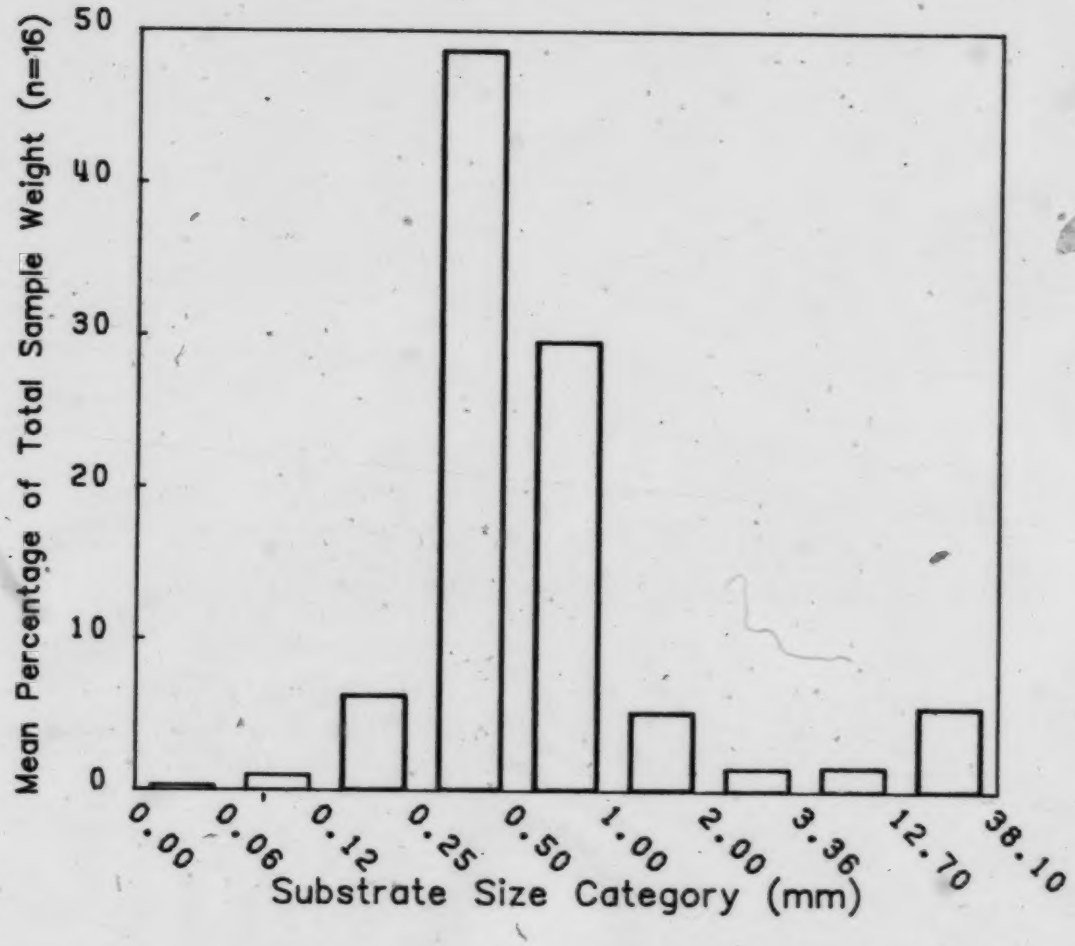

Figure II.7 Mean particle size distribution by weight (g) of substrate from the marginal sand (MS) area.

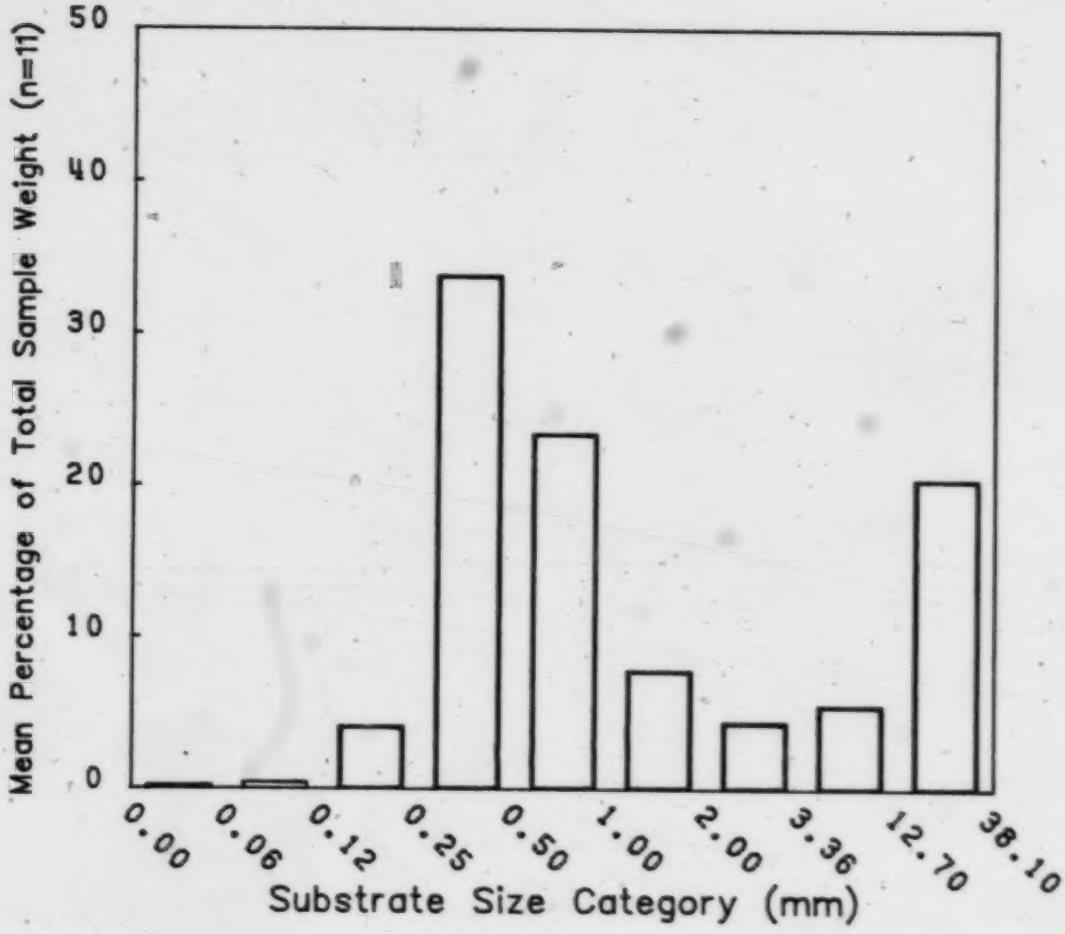

Figure II.8 Mean particle size distribution by weight (g) of substrate from the gravelly sand (GS) area.

significant differences in the total weight of substrate obtained from the three substrate types by the core-freezer (ANOVA, $F=1.99$, $p=0.15$).

Significant differences ($p<0.05$) were observed in only four of the nine particle size classes. The weight of substrate in the 12.70-38.10 mm class differed significantly between all three substrate types, GS (gravelly sand) possessing the greatest proportion of this class, and MS (marginal sand) possessing more of this class than SS (shifting sand). Particle size classes 2.00-3.36 mm and 3.36-12.70 mm were significantly more abundant in GS than in the other substrate types, and particle size class 0.50-1.00 mm was significantly more abundant in SS than in the other substrate types. No significant differences were detected amongst the finer particle size classes

The GS areas exhibited a higher proportion of the larger particle size classes, and these areas were quite distinct from the other substrate types. However, the MS areas would be expected to possess significantly more finer particles than the other substrates, since the presence of fine particles on the surface of the sediments is one of the features used to define this substrate type.

The lack of substantial differences in the distribution of particle size classes in the three substrate types was probably due in part to the historical component of the cores. The sediment collected in each core represents the depositional history of the point on the bed from which the

core was obtained. With fluctuating discharge, the nature of the material being deposited will change and, assuming no major scouring, may cover sediments laid down under very different conditions. A good example is the significantly greater weight of gravel in the 12.70-38.10 mm particle size class obtained from MS when compared to SS (Figures II.6 and II.7). The gravel found in MS was not surficial; it was contributed by a gravel layer that underlaid the area from which some MS samples were obtained. This layer occurred at a depth of approximately 20 to 30 cm below the surface of the sediment and no macroinvertebrates were obtained from this layer; however, it had a substantial effect on the particle size distribution of substrate obtained from MS areas. In fact, most of the differences between the SS and MS particle size distributions are attributable to this gravel layer.

For my objectives, I found qualitative categorization of substrate types to be a better predictor of the abundance of *R. demeijerei* and *Rheosmittia sp.* larvae than quantitative measures of particle size distribution. This suggests that the particle size distribution is only one of the factors that control the distribution of these chironomid larvae. Two other factors that might be important in determining the observed patterns of abundance exhibited by larvae of *R. demeijerei* and *Rheosmittia sp.* were: (1)the depth in the substrate in which sufficient dissolved oxygen was available, and (2)the presence of other

macroinvertebrates (especially other chironomids).

Availability of oxygen in the substrate is an important determinant of the distribution of both marine meiobenthic fauna (Coull and Bell, 1979) and freshwater hyporheic fauna (Whitman and Clark, 1982). Fenchel and Riedl (1970) define three color layers in marine quartzite sands: (1) the yellow, or oxidized layer, characterized by the presence of free oxygen and ferric iron; (2) the gray, or redox potential discontinuity (RPD) layer, characterized by the presence of both oxygen and reduced compounds; and (3) the black, or sulfide layer, characterized by the absence of free oxygen and the presence of H_2S and iron sulfides. They also indicate that these layers can move up and down on a daily basis. All three of these layers were visible in the sandy sediments of the Sand River.

To determine the relative depths of the oxidized layers in the three substrate types, measurements were made of the depth at which the gray (RPD) layer was first visible in the sediment frozen to the outside of the corer when it was removed from the substrate (Table II.6). The mean depth of the oxidized (yellow) layer represents only a minimum estimate since all depths greater than 25 cm (the maximum depth sampled) were arbitrarily given a value of 26 cm. A Kruskal-Wallis one way ANOVA by ranks (Daniel, 1978) was used to test for differences in the depth of the oxidized layers. This analysis indicated no significant difference ($H=4.71$, $p>0.05$) in the depth of the oxidized layer in MS,

Table II.6 Mean depth in the substrate of the oxidized (yellow) layer in shifting sand (SS), marginal sand (MS), and gravelly sand (GS).

Substrate Category	Mean Depth Oxygenated Layer (cm)	S.D.	n
SS	17.5	5.3	30
MS	21.9	6.0	21
GS	18.4	6.6	7

GS, or SS areas. Thus it does not appear that the depth of the oxidized layer was an important determinant of the distribution patterns of *R. demeijerei* and *Rheosmittia sp.* larvae in the Sand River.

Figure II.9 shows the abundance of chironomids other than *R. demeijerei* and *Rheosmittia* in the three substrate types. These data were analyzed in the same way as the *R. demeijerei* and *Rheosmittia sp.* data, and they indicated that significantly ($p<0.05$) more individuals of all other chironomids occur in MS and GS areas than in SS areas. This distribution is the opposite of those exhibited by larvae of *R. demeijerei* and *Rheosmittia sp.* and is consistent with the conjecture that other chironomid larvae could be exerting a negative influence on *R. demeijerei* and *Rheosmittia*

CONCLUSIONS

Larvae of *Robackia demeijerei* and *Rheosmittia sp.* were primarily associated with areas of unstable shifting sand, where their small body diameters allow them to exploit the interstitial spaces between sand grains. Other chironomids that construct tubes or tunnels in the substrate were scarce or absent from shifting sand areas, probably because of the unstable nature of these substrates.

Laboratory experiments suggest that distribution patterns exhibited by *R. demeijerei* and *Rheosmittia sp.* larvae are affected by the distribution of particle sizes in the substrate, with particles in the coarse sand size range

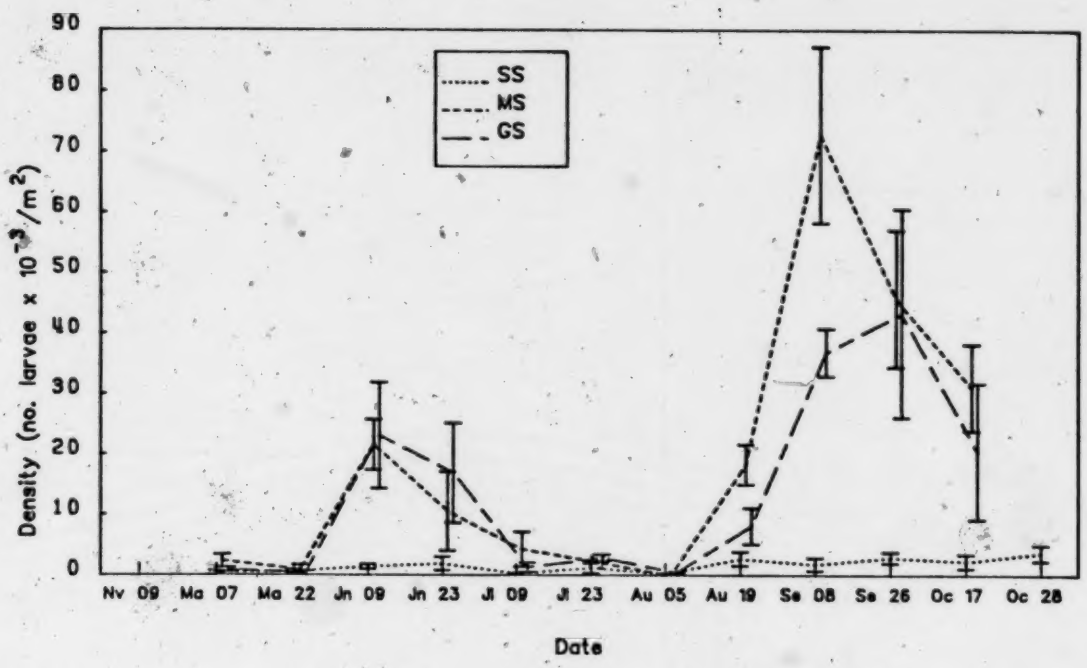

Figure II.9 Mean larval density (±S.E.) of chironomids other than *R. demeijerei* and *Rheosmittia sp.* on the three substrate types.

(0.50 - 2.00 mm) being favoured over both finer and coarser particles. However, subjective visual and tactile criteria for the separation of substrate types was a better predictor of the abundance of these species than quantitative measures of the particle size distributions of natural substrates. Other factors, such as the presence of other chironomids and the level of dissolved oxygen in the substrate, possibly influence the distribution of *R. demeijerei* and *Rheosmittia sp.*, although my data demonstrated only a negative relationship with the abundance of other chironomid larvae.

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APPENDIX 1

Construction of the Core-Freezer

The main body of the core-freezer was constructed of standard copper water pipe. Figure II.10 indicates the dimensions of the corer. The two lengths of copper pipe that made up the inner and outer walls of the corer were joined using a standard copper adapter (A) for joining 3.8 cm (1.5 in) diameter pipe to 7.6 cm (3.0 in) diameter pipe. An inner ridge on the adapter had to be removed to facilitate the use of the adapter in a backwards position. The pipes were soldered to the adapter using a high temperature silver solder. Three spacers made of 0.6 cm (0.25 in) pipe were soldered in place near the top part of the double-walled portion to keep the central tube in place. The handle was made of a solid steel rod (1.3 cm diameter), which was pushed into place through holes drilled in the outer and inner pipes. The ring (B) made of masking tape was attached 25 cm from the bottom of the corer and prevented the corer from penetrating more than 25 cm into the substrate.

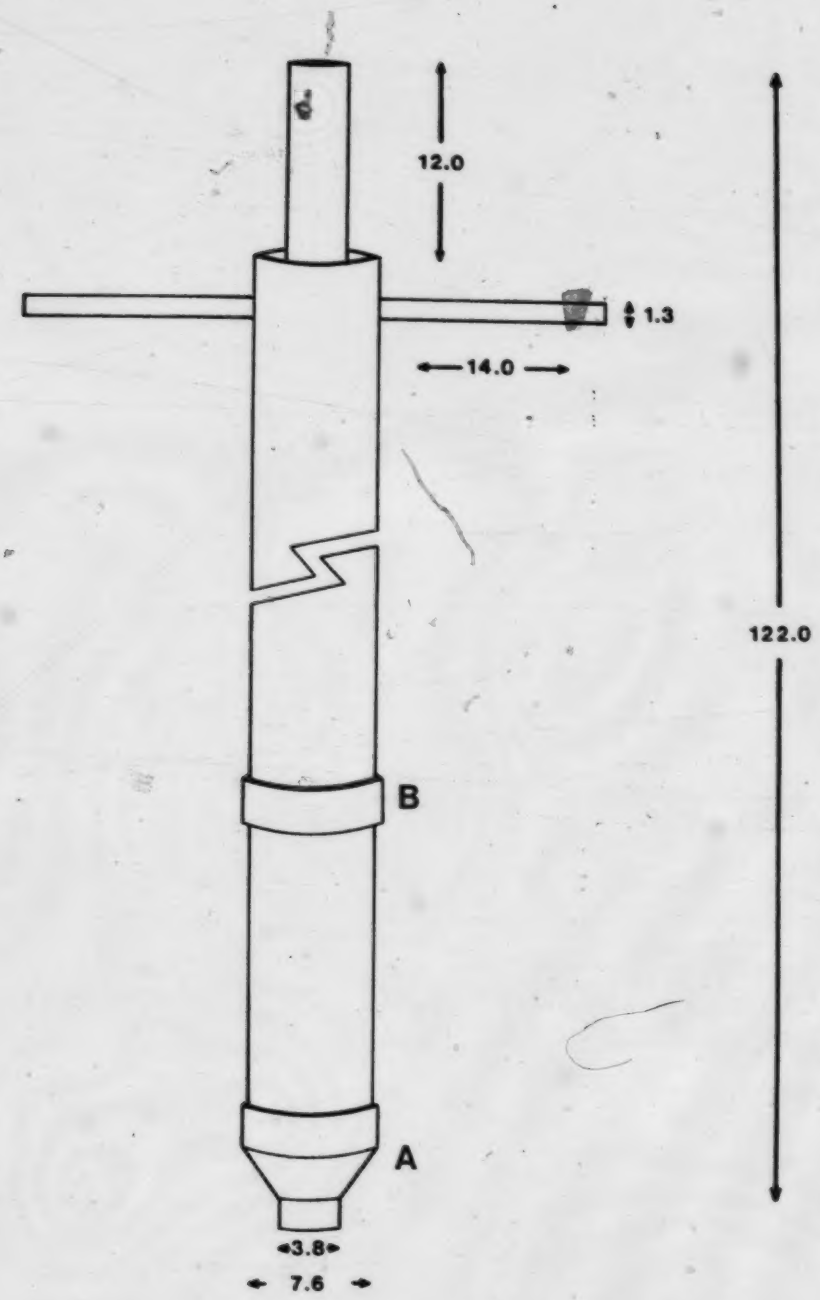

Figure II.10 The dimensions (cm) of the modified core-freezer for sampling loosely consolidated sandy substrates (all diameters are i.d.). 'A' is the adapter; 'B' is the penetration ring.

III. THE MACROINVERTEBRATES OF SHIFTING SAND AREAS: A REEVALUATION OF THEIR CONTRIBUTION TO RIVER ECOSYSTEMS.

ABSTRACT

The abundance and biomass of benthic macroinvertebrates from shifting sand areas in the bed of the Sand River in central Alberta, Canada, was examined for one year. Macroinvertebrate density was relatively high; however, total biomass was low due to the small size of most organisms. Total annual secondary production was determined for populations of the two dominant chironomid species (*Robackia demeijerei* and *Rheosmittia sp.*), and the sum of these estimates (752 mg/m²/yr) was used as an estimate of the total secondary production of benthic macroinvertebrates on shifting sand areas. Although unit area biomass and production were low relative to values reported for some other lotic habitat types, shifting sand areas and other sandy bedforms may be important if the entire river system is considered.

INTRODUCTION

Any attempt to study rivers as ecosystems will require knowledge of the functional relationships within and between communities of organisms occupying the various habitat types present in the system. Most studies conducted in streams have concentrated on organisms and communities associated with relatively coarse substrates found in riffle areas. Since large rivers are usually dominated by fine-grained materials and their characteristic bedforms (Leopold *et al.*, 1964; Hynes, 1970), riffles occupy only a small proportion of the total river bed area in these systems. Sandy sediments probably form the most common habitat types found in the beds of large rivers; however, benthic macroinvertebrates associated with these areas have seldom been studied quantitatively.

One of the most prominent types of sandy habitat are areas where the sand is being actively moved by the force of the water current. These areas are usually characterized by the presence of sand dunes, although other forms, such as plane beds and antidunes, are possible given appropriate current regimes (Leopold *et al.*, 1964; Smith, 1975). These dunes are in continuous downstream motion and present a dynamic substrate for benthic organisms. Despite this, a well-developed microfauna has been reported from shifting sand areas (Niewestnova-Shadina, 1935). However, these areas are usually characterized as unfavourable for benthic macroinvertebrates, supporting only a few individuals of a

few specialized species (Hynes, 1970).

Studies of unstable sand areas have generally supported the view that these areas support few macroinvertebrate species. However, there appear to be conflicting views on whether these areas support significant numbers of individuals. Studies of the effect of sand on smaller streams and rivers with predominantly stony bottoms have supported the view that unstable sands support few individuals (e.g. Nuttall, 1972; Lenat *et al.*, 1981). Studies of the fauna of unstable sands areas in streams with predominantly sandy bottoms (usually large streams) have yielded conflicting results, some indicating few individual macroinvertebrates (Berner, 1951; Zhadin and Gerd, 1961; Sioli, 1975; Northcote *et al.*, 1976; Seagle *et al.*, 1982) while others indicate large numbers of individuals (Zhadin and Gerd, 1961; Barton and Lock, 1979; Barton, 1980).

Perhaps more important than number of individuals are the amounts of biomass and production that shifting sand areas contribute to river ecosystems. This question has been partially addressed in only a few studies of large rivers (Berner, 1951; Zhadin and Gerd, 1961; Monakov, 1969; Northcote *et al.*, 1976; Barton and Lock, 1979).

My study was conducted to assess the biomass of benthic macroinvertebrates on shifting sand and adjacent areas and to obtain an estimate of annual secondary production for the shifting sand areas in the bed of the Sand River in Alberta, Canada. This river is not large, but the thalweg current

velocities, nature of the sediments, and the macroinvertebrate species found in the Sand River are characteristic of many large lowland rivers in North America. Thus, I feel that this an appropriate model system for studying the ecology of shifting sand substrates in rivers.

STUDY SITE

The study was carried out at the mouth of the Sand River (54°23' N, 111°02' W), in east-central Alberta. Upstream of its mouth, the Sand River is approximately 30 m wide with mean thalweg current velocities ranging from 60-150 cm/s. The mean annual discharge over the study period was approximately 16 m^3/s. The bottom of the Sand River is composed almost exclusively of sand, with silty areas occurring near the banks and with an occasional gravel bar occupying part of the bed. Mean daily summer temperature (June to September) was approximately 20°C. A more complete description of the study site is given in Chapter 1.

METHODS

Samples were collected along ten transects, set out at 5 m intervals along a 50 m stretch near the mouth of the Sand River. Samples were obtained in shifting sand areas along these transects at intervals of 5,10,20, and 30 m from the east bank, wherever possible. A series of samples was obtained prior to freeze-up in 1980 (November 9) and

approximately bi-weekly during the ice-free season of 1981 (April 23 to October 28).

The principal sampling device was a modified version of the core-freezer described by Shapiro (1958). A handled Surber sampler (mesh size 0.243 mm) was used exclusively on Nov. 9, 1980 and in conjunction with the core-freezer on May 7,1981. Construction of the core freezer and the techniques used to obtain cores are described in Chapter 2. Techniques used with the handled Surber sampler are described in Chapter 1.

Cores were kept frozen, and Surber samples were preserved in 95% ethanol for transportation and storage. Core samples were thawed, and organic material was separated from inorganic material, for both types of samples, by elutriation. The organic material was then sorted under a dissecting microscope at 12X magnification and all benthic macroinvertebrates were removed and counted. Members of the two dominant chironomid species in the shifting sand areas (*Robackia demeijerei* Krus. and *Rheosmittia sp.*) were separated by larval instar.

Mean dry weight biomass for larval populations of the two dominant chironomid species was calculated from the counts and the mean dry weights for each instar (Chapter 2). All other macroinvertebrates were separated into two categories "other chironomids" and "other organisms" and were weighed as a group to the nearest 0.002 mg on a microbalance.

Surber sampler data for the two dominant chironomids were corrected using efficiency estimates of 13% and 5% for *R. demeijerei* and *Rheosmittia sp.* respectively (Chapter 2). Total sample weights were then estimated using these corrected values.

Production estimates were obtained for larvae of each of the two dominant chironomids separately and then summed to estimate annual production for the habitat. Because of difficulty in defining the cohort structure of *Robackia demeijerei*, larval production of this species in the Sand River was estimated using the size-frequency (Hynes) method (Waters and Crawford, 1973; Waters, 1977). *Rheosmittia sp.* production was determined using the same method to maintain consistency. The 95% confidence intervals for each of the production estimates were determined using the method of Krueger and Martin (1980).

RESULTS

The mean biomass of all macroinvertebrates, all chironomids, and the two dominant chironomids obtained from shifting sand areas in the Sand River are illustrated in Figure III.1. Total invertebrate biomass was overestimated because sphaeriid (fingernail clams), which occur in significant numbers in this area, were weighed in their shells. Larvae of *R. demeijerei* and *Rheosmittia sp.* consistently contributed the majority of the chironomid (mean=94.6%, S.E.=2.3) and total invertebrate biomass

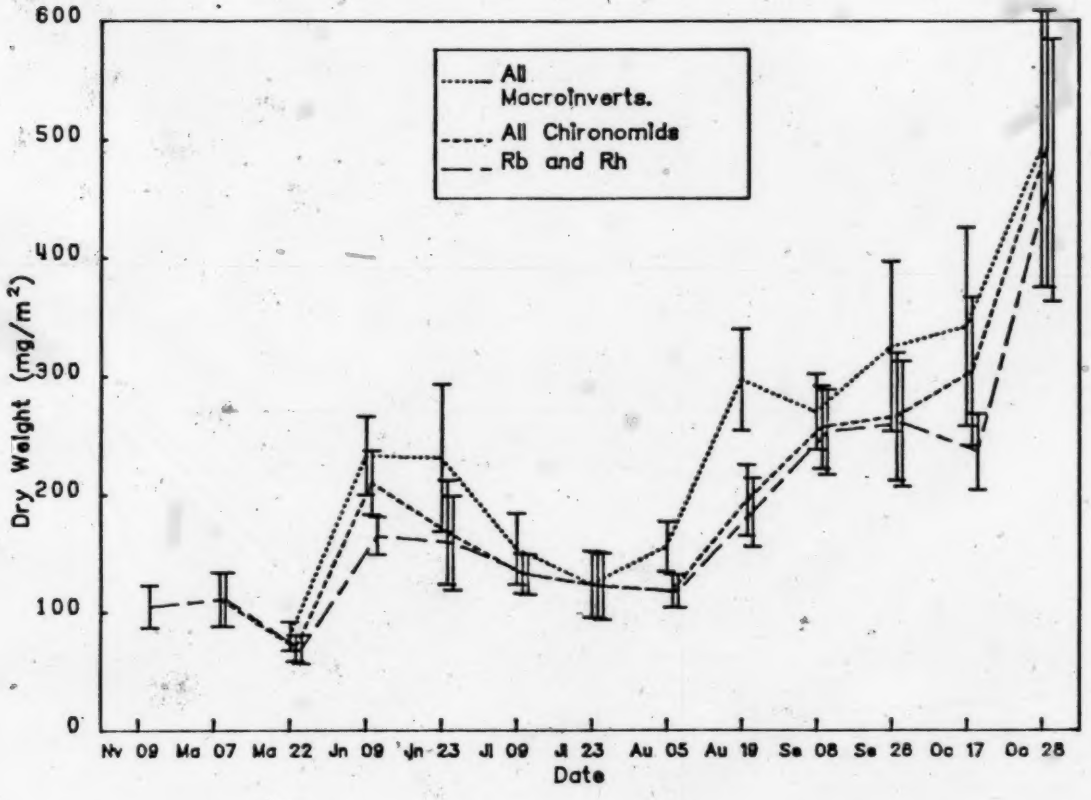

Figure III.1 Mean dry weight biomass (±S.E.) of three categories of benthic invertebrates in the Sand River; all categories are inclusive of lower categories (Rb= *R. demeijerei* and Rh= *Rheosmittia sp.*).

(mean=80.6%, S.E.=3.7). They were also the numerically dominant taxa in shifting sand areas of the Sand River (Chapter 2).

Table 1 contains the production calculations for the larval populations of each of the two dominant chironomids. The sum of the annual larval production of *R. demeijerei* and *Rheosmittia sp.* (752.03 ±144.50 mg/m²/yr) was used as a minimum estimate of total annual macroinvertebrate production from shifting sand.

DISCUSSION

Total benthic macroinvertebrate density and biomass on shifting sand areas in the Sand River was generally higher than the values reported in most other studies of unstable sandy substrates in large relatively unpolluted rivers (Table III.2). Most of the differences between the values obtained in my study and those obtained in other studies are probably attributable to differences in sampling techniques.

Unstable sandy areas tend to be dominated by small interstitial or burrowing invertebrates, which are very difficult, especially the early stages, to detect with the unaided eye. Thus, the hand-picking or live-picking techniques used by Berner (1951) and Monakov (1969) would probably greatly underestimate the number of benthic macroinvertebrates.

Most studies that report mesh sizes used in sample processing indicate mesh sizes greater than 0.50 mm. Several

Table III.1 Production (dry weight) by instar and total annual production (±95% C.I.) for the two dominant chironomids in shifting sand areas of the Sand River.

Rheosmittia sp.

Instar	No./m²	Mean wt. (mg)	No. loss	Wt. at loss (mg)	Wt. loss (mg/m²)	Prod. (mg/m²)
I+II	16464	0.0007				
			10674	0.0011	11.74	35.22
III	5790	0.0017				
			4308	0.0045	15.08	45.23
IV	1482	0.0072				
			1482	0.0072	10.67	32.01
						Σ 112.46

Annual Production = 112.46 x 2 = 224.92 ±83.47 mg/m²/yr

Robackia demeijerei

I	346	0.0015				
			-5922	0.0023	-13.62	-54.48
II	6268	0.0035				
			-939	0.0066	-6.20	-24.79
III	7207	0.0126				
			5813	0.0191	111.03	444.12
IV	1394	0.0291				
			1394	0.0291	40.56	162.26
						Σ 527.10

Annual Production = 527.10 x 1 = 527.10 ±61.03 mg/m²/yr

Table III.2 Macroinvertebrate density and dry weight biomass estimates reported from unstable sandy substrates in some large relatively unpolluted rivers (NR= not reported).

River	Author	Sampler	Mesh Size (mm)	Density (no./m²)	Biomass (mg/m²)	Comments
Missouri	Berner (1951)	Petersen grab	NR	NR	0.19-12.5¹	Hand sorted
Amur	Zhadin and Gerd (1961)	NR	NR	NR	4.1¹	Includes fine gravels
Dnieper	" "	NR	NR	NR	170¹	" "
Dniester	" "	NR	NR	1500	493¹	" "
Lena	" "	NR	NR	120-164	20.4-62.9¹	" "
Ob	" "	NR	NR	NR	2.2-39.1¹	" "
Volga	" "	NR	NR	up to 9500	960-1440¹	" "
Yenisei	" "	NR	NR	NR	62.9¹	" "
White Nile	Monakov (1969)	Petersen grab	NR	NR	0.0-200	live sorted
Fraser	Northcote *et al.* (1976)	Petersen and Ponar grabs	0.61	19-979	11-146¹	Includes gravelly sand areas
Athabasca	Barton and Lock (1979)	Ekman grab	0.18	1100-40000	60-200	
Athabasca	Barton (1980)	Airlift sampler	0.20	1675-3564	NR	
Mississippi	Seagle *et al.* (1982)	Petersen grab	0.61	200-300	NR	

¹ Dry weight approximations from wet weights using conversion factor of 0.17(Waters 1978).

studies have indicated the relative ineffectiveness of these coarse mesh sizes in retaining chironomid larvae and oligochaetes (Mason *et al.*, 1975). This situation would be aggravated by the minute size of most riverine psammophilous chironomid larvae. It is significant that the study reporting the smallest mesh size in sample processing (0.18 mm; Barton and Lock, 1979) also reported the largest numbers of invertebrates in sand areas. Because most studies have used large mesh sizes, it seems probable that the abundance and biomass of chironomidae in unstable sands have been systematically underestimated.

Although macroinvertebrate densities can be high in shifting sand areas, macroinvertebrate biomass and production estimates are usually low relative to those of many other lotic habitats (Berner, 1951; Zhadin and Gerd, 1961; Mann, 1975; Waters, 1977; Barton and Lock, 1979).

The beds of large lowland rivers are usually dominated by unstable sandy substrates (Leopold *et al.*, 1964; Barton, 1980). Zhadin and Gerd (1961) indicate that 90-95% of the beds of some rivers in the U.S.S.R. are composed of this type of substrate. In the lower reaches of the Sand River, a conservative estimate of the proportion of the river bed composed of shifting sand is 80% (based on aerial photographs and surface observations). I suggest that, although shifting sand areas support relatively little macroinvertebrate biomass or production on a per unit area basis, these areas by virtue of their large size contribute

significantly to the total macroinvertebrate biomass and production within the entire river system.

Although the role of shifting sand areas in river ecosystems is poorly known, this generally overlooked habitat is probably important because of its contribution of biomass and secondary production. The sensitivity of macroinvertebrate communities associated with shifting sand areas is unknown, but possibly some of the differences observed between my study and those of others are due to the effects of human-induced perturbations or pollution of many of the other rivers studied.

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THESIS CONCLUSION

Three species (*Pseudiron centralis*, *Robackia demeijerei*, and an undescribed species of *Rheosmittia*) of benthic macroinvertebrates dominated the shifting sand areas in the bed of the Sand River.

Pseudiron centralis is a heptageniid mayfly associated with areas of shifting sand for part of its larval life. In these areas it preys upon chironomid larvae, which it captures while foraging across the surface of actively moving sand dunes. It is univoltine and spends most of the year (July to April) in the egg stage.

Robackia demeijerei is a relatively small chironomid in the subfamily Chironominae. The larvae utilize the interstitial environment below the surface of shifting sand areas. *Robackia demeijerei* larvae have been suggested to be predaceous; however, no clear evidence of predatory behavior was obtained in my study. *Robackia demeijerei* was found to be univoltine in the Sand River, with an extended emergence period.

Rheosmittia sp. is a member of the subfamily Orthocladiinae. The genus was unrecognized until very recently, probably due to the habitats frequented by (rivers) and the small size of most members of this genus. In the Sand River, larvae of *Rheosmittia sp.* also appear to use the interstitial space available between sand grains in shifting sand areas. *Rheosmittia sp.* larvae appear to feed primarily on diatoms, probably obtained from the surface of

sand grains. This species was bivoltine in the Sand River, with a winter and a summer generation.

Populations of these three species represent more than 80% of the mean macroinvertebrate biomass associated with shifting sand areas and thus appear to be the major structural elements of macroinvertebrate communities associated with these areas in the bed of the Sand River. It appears that *Rheosmittia sp.* larvae are herbivorous exploiting psammophilic diatoms; *R. demeijerei* larvae are predators or detritivores, perhaps preying upon *Rheosmittia* or utilizing the small amounts of organic material entrained in shifting sands; and *P. centralis* larvae are predators, preying upon larvae of both *R. demeijerei* and *Rheosmittia sp.*.

Although shifting sand areas in the Sand River supported high densities of macroinvertebrates, the mean total biomass in these areas was lower on a per unit area basis than those reported from many other types of riverine habitats (Zhadin and Gerd, 1961; Barton and Lock, 1979; Seagle *et al.*, 1982). The suggestion that shifting sand areas could support relatively large amounts of macroinvertebrate production per unit area was not supported by my study, primarily because the dominant chironomids in the Sand River exhibited relatively low generation turnover rates. Macroinvertebrate production from shifting sands appears to be generally lower than values reported for entire faunas or even populations of single species in other

lotic habitats (Waters, 1977; MacFarlane and Waters, 1982).

Although the amounts of biomass and macroinvertebrate production were low in shifting sand areas, there were significant amounts. This is contrary to the suggestion that such areas support few macroinvertebrates (Berner, 1951; Hynes, 1970; Sioli, 1975) and indicates that these areas should not be ignored in studies of rivers. This is especially important if the contribution of shifting sand areas is assessed for whole reaches of the river or for the entire river system. Shifting sand areas dominate the beds of most large lowland rivers, and thus the fauna of these areas probably makes a major contribution to river ecosystems.

Further Studies

Little is known about the ecology of the biota of large rivers. I believe effective management of the river resources requires a much better understanding of the biota of these systems. I feel that my work raises some interesting questions that if addressed would contribute toward an enhanced understanding of river ecosystems.

The relationships between the three dominant macroinvertebrates in shifting sand areas of the Sand River were only briefly examined in this study; however, several questions were raised. Some of the most interesting ones involve the nature of food webs in shifting sand environments. If both *P. centralis* and *R. demejerei* larvae

are predaceous, what then is the nature of the interaction between these two species and their prey? Since *P. centralis* larvae prey on chironomids in shifting sand habitats for only a small part of the year, do these chironomid populations remain unexploited for the rest of the year?

An obvious question is whether the results of my study can be applied generally to shifting sand areas in all rivers. In terms of taxonomic composition, the macroinvertebrate fauna of shifting sand areas in the Sand River is similar to that found in other sandy rivers in North America (Chapters 1 and 2). However, given the present state of knowledge (Chapter 3), it is difficult to assess objectively whether the density, biomass, and production estimates obtained for shifting sand areas in the Sand River are truly representative of these areas in general. Further study is required to support or refute my view that most studies have failed to sample macroinvertebrates effectively in these areas.

I have attempted to compare my results only with studies of other in relatively unpolluted rivers or in unpolluted reaches of large rivers. But many of these rivers have been modified for hydroelectrical generation, flood control, and navigation. Hence, these rivers, irrespective of differences attributable to sampling methods, may support very different communities in shifting sand areas. If this is true, then the macroinvertebrate fauna of shifting sand habitats may be a important indicator of the health of a

river system. The usefulness of these animals as biomonitoring tools is potentially great, if the sampling problems could be overcome. The uniformity of shifting sand habitats over long reaches of the river bed facilitates comparisons above and below sources of human perturbation. The low diversity and large number of individuals would also probably aid in sample processing and estimating macroinvertebrate density.

The shifting sand habitat of rivers is generally considered an unfavourable habitat, because of the instability of the substrate; however, this instabilty was relatively constant and predictable over the life cycle of the benthic macroinvertebrates examined in the Sand River. Barton (1980) points out the devastating effects of fluctuating river discharges on marginal silt and bedrock areas in rivers. Areas of shifting sand appear to be relatively unaffected by moderate changes in discharge, and thus it is difficult to determine whether such areas are relatively more or less unfavourable than other river habitats. It would be interesting to determine whether the low macroinvertebrate diversity of shifting sands is a function of the physical stresses imposed by the instability of the substrate in this habitat, or whether it is a function of the long term predictability and uniformity of this habitat.

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